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PLANTS OF ARCHES NATIONAL MONUMENT

by

Bertrand F. Harrison
Stanley L. Welsh
Glen Moore

Biological Series — Vol. V, No. 1

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TABLE OF CONTENTS

Introduction 5
Annotated List of Vascular Plants 7
References 23

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Paper number 41. Brigham Young University Herbarium

Double Arch with Utah juniper in the foreground
(Photograph by D Elden Beck)

PLANTS OF ARCHES NATIONAL MONUMENT

INTRODUCTION

Located in a region of scanty rainfall, warm temperatures, and high evaporation, the Arches National Monument area supports only a limited cover of vegetation. It is hardly a scanty vegetation for the plants are numerous and the species many, but the plants are restricted to those which can endure the drought and heat of summer or which can take advantage of the infrequent rains and complete their life cycle in the brief period of relatively abundant moisture. In the general aspect of the vegetation, the grays of the desert predominate, but the vivid greens of conifers and broadleaf species are not wholly lacking, and where an additional ration of water is supplied by streams or seeps, there develops a verdure made more vivid by its contrast with the brilliant hues of the rocks and soil.

On the rocky ridges and slopes there occurs a pygmy conifer forest of juniper and pinyon pine. The juniper is more prevalent, but in locally favorable areas the pinyon pine is common. Blackbrush, ephedra, and various grasses also occur here as small islands within the forest or interspersed as a minor understory of the trees. The pygmy forest continues down from the ridges along the washes and gullies, reaching the margin of the valleys where the trees grow clustered about the bases of the great monoliths which yield them some manner of protection from the drying wind and sun. While the conifers are most abundant in this association, they are accompanied by a number of broadleaf species, notably the single leaf ash, serviceberry, Gambel oak, and wavy leaf oak.

The upland valleys and plains with their sandy well-drained soils support extensive stands of blackbrush, ephedra and Indian ricegrass, with here and there a small patch of old man sage, especially in areas of stationary dunes. Sagebrush and shadscale, so prevalent in the deserts to the west, occur here only in limited numbers. The sagebrush is restricted to the rocky slopes and washes or in the valleys where alluvium has accumulated along streams, while shadscale occurs principally on the heavier soils of the Mancos shale, Morrison, and Summerville formations. Some few junipers, pinyon pine, and Gambel oak occur in the valleys, but these plants are confined largely to the higher ridges where the geological formations are primarily sand producers. The shrubby, wavy leaf oak occurs frequently in the sandy valleys, where it acts as an effective sand binder, sending numerous branches up through the dune it helps to stabilize.

Aside from the Indian ricegrass, few grasses occur in sufficient numbers to be dominant even in local areas. Rather, they are found as scattered patches. Numerous herbaceous plants, often with showy and fragrant flowers, grow scattered among the shrubs or sometimes in limited stands in open areas. The orange-reds of the docks and the Indian paintbrush, the whites of the yucca, evening primrose, and spectacle pod, and the blues of the lupines give color and variety to the valleys, and for fragrance, there are few indeed which can equal the sand verbena.

While most of the area of the Monument is either rocky or sandy, some of the soils such as those derived from the Morrison, Mancos shale, Summerville, and Paradox formations are heavy clays with high salt and selenium concentrations. Here the vegetation differs sharply from the sandy uplands. In place of blackbrush and ephedra there are found shadscale, greasewood, seepweed, and spiny horsebrush in abundance. An occasional bush of Fremont mahonia with its spiny leaves and bright yellow blossoms is found. The long yellow stalks of the prince's plume and numerous golden heads of actinea and enceliopsis go far to make yellow the prevailing flower color of the area, but an abundance of Mohave aster which both rivals and resembles the cultivated Shasta daisy adds white and many shades of pink and lavender. The presence of this aster, prince's plume and two species of foul-smelling, pale yellow-flowered milk vetches indicates the presence of selenium, a poisonous mineral, in these soils. Two grasses—tridens and galleta grass—along with Indian paintbrush, cryptocera milkweed, and budsage, are common on these heavier soils.

Along the sides of the few streams the plants find some measure of release from the penuriousness of the climate and respond with a measure of luxuriance lacking elsewhere in

the region. Cattails, tules, reeds, and willows grow along their banks. Here is found the Fremont poplar, the only plant native to the area which justifies the name *tree*. Its size and vivid foliage are visible for great distances, and they tell the traveler that here is cooling shade and perhaps water. Many of the washes where it grows are dry much of the year, but the presence of the tree suggests that subterranean flows provide it with the necessary moisture. Tamarix, an exotic from the Mediterranean region, willows and rabbitbrush line the banks of Salt Creek for much of its length. Sedges, dwarf rushes and a few grasses are common along the water's edge. In the vicinity of Freshwater Canyon, reeds and cattails and several species of grass also are found in considerable numbers.

A saltgrass meadow east of Turnbow Cabin, along the trail to Delicate Arch, is provided with saline water from the Summerville formation. Here the salt-encrusted soil is clothed with a cover of grasses, among them saltgrass, dropseed, and rabbit-foot grass. The pickleweed and arrowgrass, common to saline regions elsewhere, are also present.

Here and there, especially along the escarpment formed by the Entrada sandstone north of Turnbow Cabin, appear small seeps where water reaches the surface after percolating along some impervious stratum. As if loath to waste a drop of the precious water, the plants cluster about these seeps, and on tiny ledges or rooted directly in the vertical walls develop small hanging gardens oblivious of the aridity of the surrounding region. The gardens tend to be layered, with specific plant species occupying definite areas along the contours of the seep. The upper layer, on the roof of the overhanging ledge, is occupied by the scarlet-red monkey flower. Below this, on the vertical face, are the endemic primrose, *Primula specuicola*, and scattered here and there the death camas. Lower down, where the lip of the garden slopes outward, the region is occupied by the columbine, helleborine orchid, maidenhair fern, bracken fern, sedges, horsetails, and various species of panic grass, bluestem, false solomon seal, poison ivy, squawbush, virgin's bower, and willow, which add to the tangle of plants that comprise these exotic gardens.

Within the limits imposed upon an area by its climate, the species which are found in any area are determined in large measure by the access which plants of other regions have to the area, or upon the development of new species within that region. The presence of lanes of migration and the absence of restrictive barriers permit plants to migrate from other regions, thus enriching the flora in numbers and species. The origins of the flora of any region must be determined from extensive field work, but from limited observations some indications of the origin of the flora of Arches Monument may be inferred. Some of the species, such as Indian ricegrass, globemallow, and sagebrush, are widely distributed throughout the Western states. Other species like the greasewood, shadscale, and cattails are common wherever the soil conditions favor their growth. Other elements of the flora with a more limited distributional range show a close relationship with the flora of the region to the south, especially to the southeast. The blackbrush, so common in the area, occurs in Utah only to the southward, the Monument area being near the northern limit of its distribution in Utah. This also applies, to a greater or lesser extent, to the wavy leaf oak, single leaf ash, dwarf milkweed, old man sage, Utah squawbush, Fremont mahonia, coldenia, side-oat grama, and numerous others.

Perhaps the lane of migration which these plants have followed is along the Colorado River or across the plateaus which border on the river, for the connection seems to be from the southward.

Endemics, those plants which have an extremely restricted range, form an interesting aspect of the flora. The primrose or Easter flower, *Primula specuicola*, and the scarlet-red monkey flower, *Mimulus eastwoodiae*, are known only from southeastern Utah and adjacent Arizona. *Lomatium latilobum* and *Atriplex garretti* were described from plants collected near the Arches area and are restricted to the nearby vicinity. *Vancleria stylosa* is found nowhere else but this region.

The impact of modern man on the region within Arches National Monument can be demonstrated by various adventive plants. These are the introduced, cultivated and weed species. One of these, the Tamarix, *Tamarix pentandra*, has already been mentioned. Other weedy species include cheatgrass and halogeton. This latter plant is a recent introduction in the area, having been introduced into Nevada during the 1930's, and then spreading slowly throughout the Western states. This plant, which has certain poisonous properties, has caused serious problems to sheepmen. Other plants have been introduced as ornamentals and shade plants in the headquarters area of the Monument; they include the red mulberry, Siberian elm, Carolina poplar, western catalpa, and black locust.

ANNOTATED LIST OF VASCULAR PLANTS

The present paper is the result of research at Arches National Monument which has extended over a period of more than fifteen years. Personnel from Brigham Young University began a survey of the scientific aspects of Arches during late April of 1947. The botanical study of the region was initiated by Dr. B. F. Harrison. The first excursion was carried out on horseback before roads were constructed into the heart of the region. Since 1947 several independent botanical excursions have been made to the Arches. During each trip the plants in flower or fruit were collected and subsequently deposited in the herbarium at Brigham Young University.

Collections have been made throughout the growing season. The area was visited in April by B. F. Harrison (1947); during May by B. F. Harrison (1948-1949), and by S. L. Welsh, G. Moore, L. B. Barnett, G. L. Pyrah, and L. M. Pitts (1963); during June by B. F. Harrison (1952) and by S. L. Welsh and G. Moore (1963); during July by S. L. Welsh and G. Moore (1963); during August by B. F. Harrison, S. L. Welsh, and G. Moore (1963); and during September by S. L. Welsh and G. Moore (1963). In the annotated list of species which follows (see below) the collectors' names will be abbreviated as follows:

BFH	B. F. Harrison
GLP	G. L. Pyrah
LBB	L. B. Barnett
LMP	L. M. Pitts
WHM	Welsh, Harrison, Moore
WM	Welsh, Moore

The following list of families, genera, and species is arranged in alphabetical order for ease of reference. Common names are provided for those species which are well known. No attempt has been made to create new names or to perpetuate the use of poorly chosen ones.

ACERACEAE - MAPLE FAMILY

Acer negundo L. Boxelder

Lower Courthouse Wash, WM 2750, 28 September 1963. Rare.

ANACARDIACEAE - CASHEW FAMILY

Rhus glabra L. Smooth sumac

Freshwater Canyon, WHM 2308, 3 August 1963. Apparently restricted to the collection locality.

Rhus trilobata Nutt. ex T. & G. Squawbush

Hanging garden, near Turnbow Cabin, GLP 43, 2 May 1963; Hanging garden, east of Turnbow Cabin, WHM 2338b, 4 August 1963. This is the common squawbush of the mesic sites throughout the Monument. The deeply lobed leaves distinguish it from the variety.

Rhus trilobata var. *simplicifolius* (Greene) Barkley Utah squawbush

Fiery Furnace, WM 2019, 4 June 1963.

Toxicodendron radicans (L.) Kuntze Poison ivy

Hanging garden, west of Turnbow Cabin, WM 1913, 2 May 1963. Poison ivy is present in moist sites throughout the region. It is especially abundant in the Fiery Furnace.

APOCYNACEAE - DOGBANE FAMILY

Apocynum cannabinum L.

Hanging garden, east of Turnbow Cabin, WHM 2336, 4 August 1963.

ASCLEPIADACEAE - MILKWEED FAMILY

Asclepias cryptoceras S. Wats. Milkweed

Turnbow Cabin, BFH 11148, 27 April 1947; Road to Devil's Garden, LBB 55, 2 May 1963. Locally common in clay soils.

Asclepias latifolia Raf.

Headquarters area, WM 2806, 30 May 1964.

Asclepias macrosperma Eastw.

Courthouse Towers, BFH 11124a, 25 April 1947; do 11381, 17 May 1949; Courthouse Wash, LMP 76, 2 May 1963; Headquarters area, WM 2000, 3 June 1963. Uncommon in sandy sites throughout the Monument.

Asclepias speciosa Torr.

Courthouse Towers, WHM 2271, 3 August 1963. Rare; possibly adventive in the Monument.

BERBERIDACEAE - BARBERRY FAMILY

Mahonia fremontii Torr. Fremont mahonia

Landscape Arch, LBB 60, 2 May 1963. This handsome shrub, with compound leaves and spinulose leaflets resembling holly leaves, has clusters of bright yellow flowers during late April and early May and bears large reddish-purple fruits during late summer. The species is infrequent throughout the Monument.

BIGNONIACEAE - BIGNONIA FAMILY

Catalpa bignonoides Walt. Catalpa

Headquarters area, WM 1998, 3 June 1963. Cultivated ornamental.

BORAGINACEAE - BORAGE FAMILY

Coldenia hispidissima (Torr.) A. Gray

Headquarters area, WM 1989, 3 June 1963. This borage is prostrate and mat-forming. It has the feature so common to the family; very spiny leaves. The plants are common along the slick-rock near Headquarters.

Cryptantha crassisepala (T. & G.) Greene Cryptantha

Courthouse Wash, BFH 11127, 25 April 1947; Landscape Arch, LMP 64, 2 May 1963. *C. crassisepala* is a delicate annual. It is abundant during early spring throughout the sandy regions of the Monument. Its abundance is, however, directly tied to the supply of moisture. If spring rains are plentiful, the plants are very numerous and are tall and robust. If there is little rainfall during the spring, the plants may be few and of small stature.

Cryptantha flava (A. Nels.) Payson

Courthouse Wash, BFH 11129, 25 April 1947; Courthouse Towers, BFH 11239, 7 May 1948; one mile west of Delicate Arch, BFH 11258, 8 May 1948; Landscape Arch, LBB 57, 2 May 1963; Windows-Balanced Rock area, LBB 44, 2 May 1963. This is probably the most common cryptantha in the Monument. The plants form clumps and bear long clusters of bright yellow flowers. It is one of the most attractive spring-flowering plants in the area.

Cryptantha fulvocanescens (A. Gray) Payson

Landscape Arch, BFH 11135, 25 April 1947.

Cryptantha longiflora (A. Nels.) Payson?

Windows-Balanced Rock area, LBB 41, 2 May 1963; Road to Devil's Garden, GLP 48, 2 May 1963.

Heliotropium convolvulaceum (Nutt.) A. Gray Heliotrope

Trail to Landscape Arch, BFH 12004, 25 June 1952; WM 2771, 24 September 1963; Courthouse Towers, WHM 2264, 3 August 1963. Locally common in sandy areas throughout the Monument.

Lappula redowskii (Hornem.) Greene Stickweed

Landscape Arch, GLP 54, 2 May 1963; Windows-Balanced Rock area, GLP 38, 2 May 1963. Ephemeral; locally common.

Lithospermum incisum Lehm.

Fiery Furnace, not collected. Rare.

CACTACEAE - CACTUS FAMILY

Echinocactus whipplei Engelm. & Bigel. Fishook cactus

Courthouse Towers, WM 1913a, 2 May 1963. Infrequent throughout the region.

Echinocereus triglochidiatus Engelm. Hedgehog cactus

Fiery Furnace, WM 2013, 4 June 1963. This is the small barrel cactus with straight spines and scarlet flowers. Locally abundant in sandy localities.

Opuntia hystricina Engelm. & Bigel.? Prickly pear

Landscape Arch, WM 2022, 4 June 1963. The stout spines borne in clusters more than half an inch apart distinguish this yellow-flowered species.

Opuntia polyacantha Haw.

Fiery Furnace, WM 2002, 4 June 1963. The slender, downward pointing spines, in clusters less than half an inch apart, are diagnostic of *O. polyacantha.*

Opuntia polyacantha var. *trichophora* (Engelm. & Bigel.) Coult.

Fiery Furnace, WM 2001, 4 June 1963. The very long, flexible spines are diagnostic of this variety. It has bright yellow flowers and is common along Salt Wash and in the Fiery Furnace Area.

Opuntia polyacantha var.?

Landscape Arch, WM 2020, 2021, 4 June 1963. The flowers of 2020 are reddish-purple in color. Specimen 2021 appears to be intermediate between typical yellow-flowered *O. polyacantha* and the reddish- purple flowered plants.

CAPPARIDACEAE - CAPER FAMILY

Cleome lutea Hook.

Alluvium near Turnbow Cabin, LBB 45, 2 May 1963.

CAPRIFOLIACEAE - HONEYSUCKLE FAMILY

Symphoricarpos longiflorus A. Gray Snowberry

Courthouse Towers, BFH 11373, 17 May 1949; Fiery Furnace WM 2018, 4 June 1963. Infrequent; well drained soils throughout the area.

CARYOPHYLLACEAE - PINK FAMILY

Arenaria feudleri A. Gray Sandwort
Windows-Balanced Rock area, LMP 43, 2 May 1963. Rare.

Silene antirrhina L. Catchfly
Fiery Furnace, WM 2015, 4 June 1963. This catchfly has a sticky area along a portion of the internode and characteristically has several small insects attached.

CHENOPODIACEAE - GOOSEFOOT FAMILY

Allenrolfea occidentalis (S. Wats.) Kuntze Pickleweed
Saltgrass Meadow, east of Turnbow Cabin, WM 2032, 4 June 1963; Turnbow Cabin, WM 2714, 28 September 1963. The jointed stem of pickleweek is succulent and has a salty, pickle-like flavor. The plants are common in the Turnbow Cabin area.

Atriplex canescens (Pursh) Nutt. Four-wing saltbush
Headquarters Area, WM 1985, 3 June 1963. The four-winged bracts of this species give it its common name. This feature, along with the size of the plant, distinguishes *A. canescens* from all other saltbushes. Infrequent in sandy areas throughout the region.

Atriplex confertifolia (Torr. & Frem.) S. Wats. Shadscale
Morrison formation, near Turnbow Cabin, WM 2047, 4 June 1963. Shadscale is the only saltbush which bears long spiny branches.

Atriplex cuneata A. Nels. Castle Valley clover
Morrison formation, near Turnbow Cabin, WM 3017, 4 June 1964. This is one of the dominant species on the Mancos shale wherever it is exposed.

Atriplex garrettii Rydb. Garrett Saltbush
Near lower Courthouse Wash, C. A. Hanson 233a, 343, 1962. Garrett saltbrush was described from near Moab, and is endemic on the talus slopes in the Colorado River Canyons. In the Monument it is common along the south boundary and in lower Courthouse Wash.

Chenopodium berlandieri Moq. Goosefoot
Freshwater Canyon, WHM 2828, 3 August 1963.

Chenopodium fremontii S. Wats.
Salt Wash, near Turnbow Cabin, WM 2723, 28 September 1963.

Echinopsilon hyssopifolium (Pall.) Moq. Bassia
Salt Wash, near Turnbow Cabin, WHM 2274, 3 August 1963.

Eurotia lanata (Pursh) Moq. Winterfat
Windows-Balanced Rock area, GLP 33, 2 May 1963; Landscape Arch, WM 2763, 29 September 1963.

Grayia brandegei A. Gray
Drainage west of Turnbow Cabin, WM 3018, 4 June 1964.

Grayia spinosa (Hook.) Moq. Hopsage
Landscape Arch, LMP 66, 2 May 1963. Uncommon.

Halogeton glomerata (Bieb.) Meyer Halogeton
Headquarters area, WM 1986, 3 June 1963. Adventive; poisonous to livestock.

Salsola kali L. Russian thistle
Headquarters area, WM 1987, 3 June 1963. Adventive.

Sarcobatus vermiculatus (Hook.) Torr. Greasewood
Alluvium along Salt Wash, near Turnbow Cabin, WM 2036, 4 June 1963.

Suaeda depressa (Pursh) S. Wats. Seepweed
Turnbow Cabin, WM 2715, 28 September 1963.

Suaeda occidentalis S. Wats.
Salt Wash, near Turnbow Cabin, WM 2722, 28 September 1963.

COMPOSITAE - SUNFLOWER FAMILY

Aster abatus Blake Aster
Headquarters, WM 2803, 29 May 1964. Rare.

Aster adscendens Lindl.
Freshwater Canyon, WHM 2299, 3 August 1963; Lower Courthouse Wash, WM 2758, 28 September 1963.

Aster arenosus Blake
Summerville formation, near Fiery Furnace, WM 2010, 4 June 1963.

Aster bigelovii A. Gray
Turnbow Cabin, WM 2718, 28 September 1963.

Aster tanacetifolius H. B. K.
Headquarters area, WM 1976, 3 June 1963; Courthouse Towers, WHM 2267, 3 August 1963.

Aster venustus M. E. Jones Mohave aster
Turnbow Cabin, BFH 11150, 27 April 1947; Road to Devil's Garden, GLP 50, 2 May 1963.

Artemisia ludoviciana Nutt.
Salt Wash, near Turnbow Cabin, WM 2728, 28 September 1963.

Artemisia ludoviciana ssp. *mexicana* (Willd.) Keck
Salt Wash Canyon, on slick rock, WM 2734, 28 September 1963.

Artemisia spinescens D. C. Eaton Budsage
Near Turnbow Cabin, on Morrison formation, WM 2048, 4 June 1963.

Artemisia tridentata Nutt. Big sagebrush
Courthouse Towers, WM 2256, 3 August 1963; Salt Wash, sandy alluvium, WM 2737, 28 September 1963. Locally abundant in scattered areas of the Monument.

Aster abatus Blake Aster
Headquarters, WM 2803, 29 May 1964. Rare.

Aster adscendens Lindl.
Freshwater Canyon, WHM 2299, 3 August 1963; Lower Courthouse Wash, WM 2758, 28 September 1963.

Aster arenosus Blake
Summerville formation, near Fiery Furnace, WM 2010, 4 June 1963.

Aster bigelovii A. Gray
Turnbow Cabin, WM 2718, 28 September 1963.

Aster tanacetifolius H. B. K.
Headquarters area, WM 1976, 3 June 1963; Courthouse Towers, WHM 2267, 3 August 1963.

Aster venustus M. E. Jones Mohave aster
Turnbow Cabin, BFH 11150, 27 April 1947; Road to Devil's Garden, GLP 50, 2 May 1963. Locally common in heavy soils of the Mancos shale, and other clay formations.

Baeharis emoryi A. Gray
Lower Courthouse Wash, WM 2762, 28 September 1963. Rare in the Monument but common along the Colorado River.

Bahia nudicaulis A. Gray
Turnbow Cabin, BFH 11398, 18 May 1949; Morrison Formation, near Fiery Furnace, WM 2007, 4 June 1963. Locally common on the Morrison formation.

Brickellia longifolia S. Wats. Brickellbush
Sandy slope east of Salt Wash, WM 2738, 28 September 1963; Lower Courthouse Wash, WM 2753, 28 September 1963. Locally common along the Courthouse Wash drainage.

Brickellia scabra (A. Gray) A. Nels.
Freshwater Canyon, WHM 2298, 3 August 1963.

Chrysopsis foliosa Nutt. Golden aster
Headquarters area, BFH 11121, 25 April 1947; Courthouse Wash, LMP 68, 2 May 1963; Salt Wash near Turnbow Cabin, WHM 2289, 3 August 1963; WHM 2324, 3 August 1963; WM 2740, 28 September 1963. Common throughout the Monument.

Chrysothamnus nauseosus (Pall.) Britt. ssp. *graveolens* (Nutt.) H. & C. Rabbitbrush
Turnbow Cabin, WM 2711, 28 September 1963. This is the common big rabbitbrush in the Monument.

Chrysothamnus nauseosus ssp. *leiospermus* (A. Gray) H. & C.
Vicinity of Landscape Arch, WM 2768, 29 September 1963. Rare.

Chrysothamnus nauseosus ssp. *pinifolius* (Greene) H. & C.
Vicinity of Landscape Arch, WM 2765, 29 September 1963. Rare.

Chrysothamnus parryi (A. Gray) Greene
Vicinity of Landscape Arch, WM 2764, 29 September 1963. Rare; this species has the largest flowers of any rabbitbrush in the vicinity. The involucral bracts are in excess of 15 mm in length.

Chrysothamnus viscidiflorus (Hook.) Nutt.
Salt Wash, near Turnbow Cabin, WHM 2285, 3 August 1963.

Chrysothamnus viscidiflorus ssp. *linifolius* (Greene) H. & C.
Salt Wash, near Turnbow Cabin, WM 2727, 28 September 1963.

Chrysothamnus viscidiflorus ssp. *stenophyllus* (A. Gray) H. & C.
Freshwater Canyon, WHM 2294, 3 August 1963.

Cirsium undulatum (Nutt.) Spreng. Thistle
Salt Wash, near Turnbow Cabin, WHM 2281, 3 August 1963. Rare.

Cirsium sp.
Hanging Garden, north of trail to Delicate Arch, WM 2207, 13 June 1963; WHM 2331, 4 August 1963; Hanging garden, east side of Salt Wash Canyon, WM 2742, 28 September 1963. Evidently endemic to the hanging gardens in the region.

Conyza canadensis (L.) Cronq.
Courthouse Towers, WHM 2261, 3 August 1963. Probably adventive.

Crepis runcinata T. & G.
Saltgrass meadow, east of Turnbow Cabin, WM 2044, 4 June 1963. Rare; apparently limited to the collection locality in the Monument.

Dicoria canescens A. Gray ex. Torr.
Sandy areas south of Turnbow Cabin, WM 2723, 28 September 1963. Common along roadsides and drainages throughout the area.

Encelia frutescens A. Gray
Headquarters area, WM 1994, 3 June 1963. The large, hemispheric clumps of *Encelia* are showy at full anthesis. Common on the slick rock near Headquarters.

Enceliopsis nutans (Eastw.) A. Nels.
Turnbow Cabin, BFH 11148a, 27 April 1947; road to Devil's Garden, GLP 54, 2 May 1963. Locally common on the heavy soils of the Mancos Shale formation.

Erigeron bellidastrum Nutt.
Courthouse Wash, GLP 65, 2 May 1963; Landscape Arch, LBB 59, 2 May 1963. Locally common in sandy areas throughout the region.

Erigeron divergens T. & G.
Hanging garden, near Turnbow Cabin, WM 2043, 4 June 1963.

Erigeron utahensis A. Gray
Headquarters area, BFH 11363, 27 April 1949; WM 1992, 3 June 1963. Widely distributed in the Monument; uncommon.

Flaveria campestris J. R. Johnston
Sandy alluvium along stream course, lower Courthouse Wash, WM 2751, 28 September 1963. As far as can be determined, this species has not been reported for Utah previously. It has been reported by various authors (Harrington, 1954; Fernald, 1950; Gleason, 1952) as occurring in Colorado, New Mexico, Mexico and adventive eastward to Missouri. The nature of its occurrence in Utah is not known. It is locally abundant in the region where it was collected. Several disjunct stands were noted.

Franseria acanthicarpa (Hook.) Coville Bursage
Turnbow Cabin, WM 2712, 28 September 1963. Widely distributed in disturbed sandy sites. The plants flower in late summer and produce the characteristic burs from early to late fall.

Gaillardia pinnatifida Torr.
Landscape Arch, BFH 11411, 19 May 1949; Morrison formation, near Fiery Furnace, WM 2009, 4 June 1963. Locally common; a plant with showy yellow flowers.

Gaillardia spathulata A. Gray
Near Turnbow Cabin, WM 2049, 4 June 1963. Locally abundant; disturbed roadsides.

Grindelia aphanactis Rydb. Gumweed
Freshwater Canyon, WHM 2296, 3 August 1963; Salt Wash, north of Freshwater Canyon, WM 2730, 28 September 1963. Common along stream courses throughout the region.

Gutierrezia microcephala DC. Snakeweed
Courthouse Towers, WHM 2259, 3 August 1963. Common throughout the region. The small flowers distinguish this species from the next.

Gutierrezia sarothrae (Pursh) Britt. & Rusby
Courthouse Towers, WHM 2258, 3 August 1963; Turnbow Cabin, WM 2715, 28 September 1963; Salt Wash, WM 2743, 28 September 1963. Common throughout the region.

Haplopappus armerioides (Nutt.) A. Gray
Windows Area, BFH 11393, 18 May 1949; Fiery Furnace, WM 2014, 4 June 1963. Uncommon.

Haplopappus nuttallii T. & G.
Headquarters area, WM 1990, 3 June 1963. Uncommon.

Haplopappus sp.
Salt Wash near Turnbow Cabin, WHM 2284, 3 August 1963; south of Turnbow Cabin, WM 2721, 28 September 1963. Common along the moist sandy banks of stream courses.

Helianthus annuus L. Sunflower
Salt Wash, near Turnbow Cabin, WM 2725, 28 September 1963.

Helianthus anomalus Blake
Lower Courthouse Wash, WM 2759, 28 September 1963. Locally abundant; dry sandy flood plains.

Helianthus petiolaris Nutt.
Alluvium, near Turnbow Cabin, WM 2050, 4 June 1963; Salt Wash, north of Freshwater Canyon, WM 2726, 28 September 1963. Infrequent in disturbed sandy sites.

Heterotheca subaxillaris (Lam.) Britt. & Rusby Telegraph weed
Courthouse Towers, WM 2744, 28 September 1963. This plant was growing along a roadside. It has bright yellow flowers and grows to a height of 3 to 4 feet. The genus has not been

reported for Utah by the major floras and there is reason to believe that this collection represents a new record. The species ranges from southern California and southern Arizona eastward to Delaware and Florida (Kearney & Peebles, 1950, Abrams & Ferris, 1960). Only two specimens were noted, and it is probable that they represent adventives from the more southern range of the species.

Hymenoxys acaulis (Pursh) Parker var. *ivesiana* (Greene) Parker

Turnbow Cabin vicinity, BFH 11151, 27 April 1947; Headquarters area, BFH 11250, 8 May 1948; WM 1988, 3 June 1963; Windows-Balanced Rock area, LBB 33, 2 May 1963; Courthouse Wash, GLP 63, 2 May 1963. Common in sandy areas throughout the Monument. The showy, bright yellow flowers of this plant make it one of the most attractive of the spring flowers.

Lygodesmia grandiflora (Nutt.) T. & G. Skeleton weed

Alluvium near Fiery Furnace, WM 2006, 4 June 1963. Locally common.

Malacothrix sonchoides (Nutt.) T. & G.

Headquarters area, BFH 11251, 8 May 1948; Windows-Balanced Rock area, GLP 29, 2 May 1963. Uncommon.

Senecio multicapitatus Greenm. ex Rydb. Groundsel

Salt Wash, near Turnbow Cabin, WHM 2275, 3 August 1963; Salt Wash above Freshwater Canyon, WM 2724, 28 September 1963; Lower Courthouse Wash, WM 2754, 28 September 1963. Locally common along stream courses throughout the region.

Senecio multilobatus T. & G.

Along trail to Delicate Arch, Welsh 1921, 11 May 1963.

Solidago altissima L. Goldenrod

Hanging garden, east of Turnbow Cabin, WHM 2333, 4 August 1963; hanging garden, east side of Salt Wash Canyon, WM 2738, 28 September 1963. Common in moist hanging gardens.

Solidago canadensis L.

Salt Wash, near Turnbow Cabin, WHM 2283, 3 August 1963.

Solidago occidentalis (Nutt.) T. & G.

Salt Wash, near Turnbow Cabin, WHM 2277, 3 August 1963; Turnbow Cabin, WM 2720, 28 September 1963. Locally common in moist sites.

Solidago petradoria Blake Rock goldenrod

Vicinity of Landscape Arch, WM 2769, 29 September 1963. Rare.

Sonchus aspera (L.) Hill Sowthistle

Saltgrass meadow, east of Turnbow Cabin, WM 2035, 4 June 1963. Locally common.

Stephanomeria exigua Nutt. Wirelettuce

Headquarters area, WM 1981, 3 June 1963. Abundant annual in the flat area surrounding Headquarters.

Stephanomeria pauciflora (Torr.) A. Nels.

Hanging garden, east of Turnbow Cabin, WHM 2338, 4 August 1963; Courthouse Towers Area, WHM 2263, 3 August 1963. Locally common in rocky situations.

Stephanomeria tenuifolia (Torr.) H. M. Hall?

Headquarters area, WM 1991, 3 June 1963. The specimen is in vegetative condition and the diagnostic characteristics are lacking.

Taraxacum officinale Weber. Dandelion

Courthouse Wash, WM 2810, 30 May 1964. Old World adventive.

Tetradymia spinosa Hook & Arn. Horsebrush

Salt Wash, BFH 11140, 26 April 1947; two miles west of Turnbow Cabin; 11409, 18 May 1949; Morrison formation near Fiery Furnace, WM 2005, 4 June 1963. Locally common on the clay soils of the Morrison and Mancos shale formations.

Townsendia incana A. Gray

Courthouse Towers, BFH 11374, 17 May 1949; Courthouse Wash, LMP 74, 2 May 1963. Uncommon.

Tragopogon dubius Scop.

Courthouse Wash, WM 2813, 30 May 1964. Adventive from Europe.

Vancleva stylosa (Eastw.) Greene

Courthouse Towers, WHM 2268, 3 August 1963; Turnbow Cabin, WM 2717, 28 September 1963. Common throughout the Monument.

Wyethia scabra Hook. Mule's ears

Headquarters area, BFH 11159a, 27 April 1947; Courthouse Wash, LBB 71, 2 May 1963. A coarse clump-forming plant with large yellow flowers. Common on the slick-rock near Headquarters and on alluvium in Salt Valley.

Xanthium pennsylvanicum Wallr. Cocklebur

Salt Wash, near Turnbow Cabin, WHM 2286, 3 August 1963.

CONVOLVULACEAE - MORNING-GLORY FAMILY

Cuscuta sp.
Salt Wash, east of Turnbow Cabin, WHM 2345, 4 August 1963. The plant is in vegetative condition and the specific diagnostic characteristics are missing. It is parasitic on *Grindelia aphanactis.*

CRUCIFERAE - MUSTARD FAMILY

Arabis perennans S. Wats.
Salt Wash, BFH 11140a, 26 April 1947.

Arabis pulchra M. E. Jones
Courthouse Towers, BFH 11125, 25 April 1947; Windows area, BFH 11395, 18 May 1949; Windows-Balanced Rock area, GLP 37, 2 May 1963; near Turnbow Cabin, LMP 56, 2 May 1963. Locally common.

Descurainia pinnata (Walt.) Britt.
Landscape Arch, GLP 52, 2 May 1963. Seasonally abundant in sandy areas, especially in the juniper-pinyon forest.

Dithyrea wislizenii Engelm. Spectacle Pod
Courthouse Wash, BFH 11128, 25 April 1947; Windows-Balanced Rock area, GLP 35, 2 May 1963; Landscape Arch, LMP 65, 2 May 1963. Abundant in sandy areas throughout the Monument.

Draba cuneifolia Nutt.
Fiery Furnace, WM 2774, 10 May 1964.

Erysimum asperum (Nutt.) DC. Wallflower
Windows-Balanced Rock area, LMP 40, 2 May 1963.

Lepidium densiflorum Schrad.
Fiery Furnace, WM 2773, 10 May 1964.

Lepidium montanum Nutt. Peppergrass
Courthouse Towers, BFH 11240, 7 May 1948; Windows-Balanced Rock area, LBB 40, 2 May 1963; Landscape Arch, GLP 55, 2 May 1963. Abundant in sandy sites.

Malcolmia africana (L.) R. Br.
Courthouse Wash, WM 2808, 30 May 1964. Old World weed.

Physaria australis (Payson) Rollins Bladderpod
Windows area, BFH 11159, 27 April 1947; BFH 11390, 18 May 1949; Windows-Balanced Rock area, LBB 42, 2 May 1963; near Turnbow Cabin, GLP 39, 2 May 1963. Uncommon.

Rorippa nasturtium-aquaticum (L.) Schinz & Thel. Watercress
Salt Wash, near Turnbow Cabin, WHM 2279, 3 August 1963. Rare; adventive from the Old World.

Stanleya pinnata (Pursh) Britt. Prince's plume
Headquarters area, BFH 11388, 18 May 1949; Courthouse Wash, LBB 65, 2 May 1963. Common on clay and silt alluvium derived from the Carmel, Mancos shale, Morrison, Summerville, and Paradox formations. The species is an indicator of seleniferous soils. The tall yellow racemes stand out in bold contrast to the surroundings. This is one of the most striking of the spring and summer flowers in the Arches.

Streptanthella longirostris (S. Wats.) Rydb.
Headquarters area, BFH 11371, 17 May 1949; Windows-Balanced Rock area, LBB 43, 2 May 1963; Landscape Arch, LMP 62, 2 May 1963. Annual; locally abundant, especially in sandy soils in the juniper-pinyon community.

Streptanthus cordatus Nutt.
Windows area, BFH 11161, 27 April 1947.

Thelypodium integrifolium (Nutt.) Endl.
Hanging gardens, north of trail to Delicate Arch; WHM 2337, 4 August 1963. Biennial; plants 3 to 7 feet tall with dense racemes of whitish flowers. Locally abundant.

CYPERACEAE - SEDGE FAMILY

Carex aquatilis Wahl. Sedge
Seep near Turnbow Cabin, GLP 52, 2 May 1963.

Carex foenea Willd.?
Seep near Turnbow Cabin, GLP 42, 2 May 1963.

Carex garberi Fern.
Hanging garden, near Turnbow Cabin, BFH 11144, 27 April 1947; do 11402, 18 May 1949; LMP 51, 2 May 1963. Restricted to the moist hanging gardens where they occupy the lip of the garden along with muhly grass and heleborine orchids.

Carex hystricina Muhl.
Freshwater Canyon, WHM 2300, 3 August 1963. Abundant around pools in Freshwater Canyon.

Eleocharis palustris (L.) R. & S.? Spike rush
Seep, near Turnbow Cabin, LBB 49, 2 May 1963.

Scirpus americanus Pers. Bulrush
Seep, near Turnbow Cabin, LBB 46, 2 May 1963; Courthouse Wash, LBB 72, 2 May 1963.

Abundant along moist drainages throughout the Monument.

Scirpus validus Vahl.
Salt Wash, near Turnbow Cabin, WHM 2276, 3 August 1963.

ELAEAGNACEAE - OLEASTER FAMILY

Elaeagnus angustifolia L. Russian Olive
Lower Courthouse Wash, WM 2748, 28 September 1963. Adventive; becoming established at several places in the Monument.

EQUISETACEAE - HORSETAIL FAMILY

Equisetum arvensis L. Horsetail
Salt Wash, near Turnbow Cabin, WHM 2282, 3 August 1963. Uncommon.

Equisetum kansanum Schaffn.
Seep, near Turnbow Cabin, LBB 51, 2 May 1963.

Equisetum praltum Raf.
Freshwater Canyon, WHM 2293, 3 August 1963.

EUPHORBIACEAE - SPURGE FAMILY

Euphorbia fendleri T. & G. Spurge
Courthouse Wash, GLP 61, 2 May 1963.

Euphorbia parryi Engelm.
Landscape Arch vicinity, WM 2025, 4 June 1963; Sandy alluvium near Turnbow Cabin, WM 2710, 28 September 1963. Common in sandy soils.

Euphorbia robusta (Engelm.) Small
Hanging garden, near Turnbow Cabin, BFH 11143, 27 April 1947; do 11255, 8 May 1948; LMP 55, 2 May 1963. Common; hanging gardens throughout the Monument.

FAGACEAE - BEECH FAMILY

Quercus gambelii Nutt. Gambel oak
Freshwater Canyon, BFH 11146, 27 April, 1947; LBB 48, 2 May 1963; WHM 2307, 3 August 1963. Locally common in more mesic sites along the stream courses.

Quercus undulata Torr. Wavy leaf oak
Courthouse Towers, BFH 11124, 25 April 1947; Headquarters area, 11387, 17 May 1949; Courthouse Wash, GLP 66, 2 May 1963; Landscape Arch, GLP 56, 2 May 1963. A dominant species in the plant communities on stabilized dunes. A specimen from lower Courthouse Wash (WM 2749, 28 September 1963) is from an erect form of this complex group. It grows on the shelf rock along the wash.

GENTIANACEAE - GENTIAN FAMILY

Swertia albomarginata (S. Wats.) Kuntze Green gentian
Dunes over Morrison formation, east of Turnbow Cabin, WHM 2343, 4 August 1963. Uncommon; noted only at this locality.

GERANIACEAE - GERANIUM FAMILY

Erodium cicutarium (L.) L'Her Storksbill
Fiery Furnace, WM 2016, 4 June 1963. Locally abundant in disturbed soil; adventive.

GNETACEAE - JOINTFIR FAMILY

Ephedra torreyana S. Wats. Mormon tea
Headquarters area, BFH 11252, 8 May 1948; Courthouse Towers, BFH 11385, 11386, 17 May 1949; Courthouse Wash, GLP 59, 2 May 1963. Less common than the next species and distinguished by its sprawling form and olive-drab branchlets.

Ephedra viridis Coville
Courthouse Towers area, BFH 11372, 17 May 1949; Trail to Landscape Arch, BFH 12007, 25 June 1952; Windows-Balanced Rock area, BFH 11261, 9 May 1948; GLP 32, 2 May 1963. A dominant plant in the communities on stabilized dunes. The erect, bright green branchlets distinguish this species from the former.

GRAMINEAE - GRASS FAMILY

Agropyron desertorum (Fisch.) Schult. Crested wheatgrass
Klondike Wash, WM 2052, 4 June 1963. Adventive forage plant; rare.

Agropyron smithii Rydb.
Courthouse Wash, WM 2809, 30 May 1964.

Agropyron trachycaulum (Linke) Malte Slender wheatgrass
Fiery Furnace, WM 2003, 4 June 1963. Locally common in more shaded mesic sites.

Agrostis alba L. Redtop
Freshwater Canyon, WHM 2295, 3 August 1963. Moist places; adventive from the Old World.

Andropogon scoparius Michx. Little bluestem
Sandstone slope, east side of Salt Wash, WM 2736, 28 September 1963; Lower Courthouse

Wash; WM 2761, 28 September. This species is characteristic of the short-grass prairie of the Great Plains. Arches National Monument is at or near the northern limits of the range of the species in Utah.

Aristida fendleriana Steud. Three-awn grass
Courthouse Towers, BFH 11237, 7 May 1948; Trail to Landscape Arch, BFH 12005, 25 June 1952; Windows-Balanced Rock area, BFH 11980, 16 May 1952; LMP 41, 2 May 1963; WHM 2330, 3 August 1963. Probably the most abundant three-awn species in the Monument.

Aristida glauca (Nees) Walp.
Four miles northeast of Windows area, BFH 12017, 25 June 1952.

Aristida longiseta Steud.
Landscape Arch, BFH 11413, 19 May 1949; Courthouse Towers, WHM 2266, 3 August 1963. Uncommon.

Bouteloua barbata Lag.
Headquarters area, WM 2531, 18 August 1963. Locally abundant.

Bouteloua curtipendula (Michx.) Torr. Side-oats grama
Headquarters area, BFH 11365, 17 May 1949; Freshwater Canyon, WHM 2313, 3 August 1963. Rare; a plant more characteristic of the short-grass praries of the Great Plains.

Bromus marginatus Nees
Courthouse Wash, WM 2818, 30 May 1964.

Bromus tectorum L. Cheatgrass
Windows-Balanced Rock area, LMP 44, 2 May 1963. Adventive from the Old World; uncommon.

Cenchrus pauciflorus Benth. Sandbur
Lower Courthouse Wash, WM 2756, 28 September 1963. Uncommon; the spines of the burs are retrorsely barbed and are difficult to remove from the skin or from clothing.

Dactylis glomerata L. Orchard grass
Freshwater Canyon, WHM 2315, 3 August 1963. Adventive forage grass from the Old World; rare.

Distichlis stricta (Torr.) Rydb. Saltgrass
Saline seep, east of Turnbow Cabin, WM 2031, 4 June 1963. Locally abundant.

Echinochloa crus-galli (L.) Beauv. Barnyard grass
Headquarters area, WM 2745, 28 September 1963. Adventive weed.

Elymus canadensis L. Canada wild-rye
Salt Wash, near Turnbow Cabin, WHM 2278, 3 August 1963. Rare.

Elymus salinus M. E. Jones
Freshwater Canyon, WHM 2297, 3 August 1963. Locally common on dry rocky ridges.

Festuca octoflora Walt. Six-weeks fescue
Turnbow Cabin, BFH 11156, 27 April 1947; Windows-Balanced Rock area, GLP 34, 2 May 1963; Landscape Arch, LBB 62, 2 May 1963. Common to abundant throughout the region.

Glyceria striata (Lam.) Hitchc. Mannagrass
Freshwater Canyon, WHM 2317, 3 August 1963. Common.

Hilaria jamesii (Torr.) Benth. Galleta
Turnbow Cabin, BFH 11153, 27 April 1947; Courthouse Wash, GLP 60, 2 May 1963; Road to Devil's Garden, GLP 46, 2 May 1963. Widely distributed in the Monument, but seldom abundant.

Hordeum jubatum L. Foxtail barley
Freshwater Canyon WHM 2314, 3 August 1963. Rare.

Muhlenbergia andina (Nutt.) Hitchc. Muhly grass
Freshwater Canyon, WHM 2311, 3 August 1963.

Muhlenbergia asperifolia (Nees & Mey.) Parodi
Below Delicate Arch, BFH 12018, 26 June 1952; Salt Wash, near Turnbow Cabin, WHM 2273, 3 August 1963. Abundant in saline areas along stream courses.

Muhlenbergia curtifolia Scribn.
Hanging garden, east of Turnbow Cabin, WHM 2334, 4 August 1963; Lower Courthouse Wash, WM 2755, 28 September 1963. Dry hillside; rare.

Muhlenbergia mexicana (L.) Trin.
Freshwater Canyon, WHM 2302; 3 August 1963.

Muhlenbergia pungens Thurb. ex A. Gray
Windows area, WHM 2329, 3 August 1963. Common in sandy areas.

Munroa squarrosa (Nutt.) Torr.
Courthouse Towers, WHM 2257, 3 August 1963. Locally common along roadsides; probably adventive.

X *Oryzopsis bloomeri* (Boland) Ricker Ricegrass
Landscape Arch trail, BFH 12011, 25 June

1952. Rare, a putative hybrid between *O. hymenoides* and *Stipa comata*.

Oryzopsis hymenoides (R. & S.) Ricker
Indian ricegrass
Courthouse Wash, LMP 70, 77, 2 May 1963. Abundant, the dominant grass species on the sandy areas of the Monument.

Panicum tennesscensis Ashe Panic grass
Four miles northeast of Windows area, BFH 12014, 26 June 1952; Hanging garden, near Turnbow Cabin, WM 2042, 4 June 1963; Freshwater Canyon, WHM 2303, 3 August 1963. Restricted to the lip of hanging gardens; locally abundant.

Phleum pratense L. Timothy
Freshwater Canyon, WHM 2316, 3 August 1963. Rare; adventive forage species from the Old World.

Phragmites communis L. Common reed
Salt Wash, near Turnbow Cabin, WHM 2291, 3 August 1963. Occurring in disjunct stands along the moist stream courses and in the hanging gardens. The stems were utilized by Indians in making arrow foreshafts.

Poa longiligula Scribn. & Will Mutton grass
Hanging garden, 1 mile east of Turnbow Cabin, BFH 11403, 18 May 1949; Windows- Balanced Rock area, BFH 11130, 25 April 1947; LBB 34, 2 May 1963; GLP 30, 2 May 1963; LMP 46, 2 May 1963; Landscape Arch, BFH 11471, 19 May 1949; LBB 56, 2 May 1963. Locally common, especially in sandy regions, but never abundant.

Poa pratensis L. Bluegrass
Courthouse Wash, WM 2816, 30 May 1964. Adventive.

Polypogon monspeliensis (L.) Desf.
Rabbitfoot grass
Saltgrass meadow, east of Turnbow Cabin, WM 2034, 4 June 1963; Salt Wash, near Turnbow Cabin, WHM 2272, 3 August 1963. Locally abundant in moist sandy areas.

Puccinellia distans (L.) Parl.
Saltgrass meadow, east of Turnbow Cabin, WM 2030, 4 June 1963.

Setaria viridis (L.) Beauv. Green bristlegrass
Headquarters area, WHM 2346, 4 August 1963. Rare.

Sitanion hystrix (Nutt.) J. G. Smith
Squirreltail grass
Headquarters area, BFH 11389, 18 May 1949; Windows area, BFH 11394, 18 May 1949; near Turnbow Cabin, LMP 53, 2 May 1963. Widely distributed in the Monument, but rarely common.

Sphenopholis obtusata (Michx.) Scribn.
Freshwater Canyon, WHM 2312, 3 August 1963. Rare.

Sporobolus airoides (Torr.) Torr. Dropseed
Saltgrass meadow, east of Turnbow Cabin, WM 2041, 4 June 1963. Locally common.

Sporobolus contractus Hitchc.
Four miles northeast of Windows area, BFH 12012, 25 June 1952; Headquarters area, WM 1984, 3 June 1963. Locally common in sandy areas.

Sporobolus cryptandrus (Torr.) A. Gray
Vicinity of Landscape Arch, WM 2766, 29 September 1963. Widely distributed throughout the Monument and locally common.

Sporobolus flexuosus (Thurb.) Rydb.
Trail to Landscape Arch, BFH 12002, 25 June 1952. In sandy soils this plant is probably second in abundance only to Indian ricegrass.

Sporobolus giganteus Nash
Courthouse Towers, WHM 2270, 3 August 1963. Locally common along sandy roadsides and to some extent in the dune areas.

Stipa comata Trin. & Rupr.
Needle-and-thread grass
Windows area, BFH 11979, 16 May 1952; Landscape Arch, WM 2028a, 4 June 1963. Abundant locally in the vicinity of Landscape Arch and in a few other isolated areas.

Stipa speciosa Trin. & Rupr.
Windows area, BFH 11978, 16 May 1952.

Tridens pilosus (Buckl.) Hitchc.
Turnbow Cabin area, BFH 11155, 27 April 1947; do 11404, 18 May 1949; Headquarters area, BFH 11369, 17 May 1949.

Tridens pulchellus (H. B. K.) Hitchc. ex Jepson
Headquarters area, BFH 11368, 17 May 1949.

Triticum aestivum L. Wheat
Headquarters area, WM 1979, 3 June 1963. Adventive cereal grain.

HYDROPHYLLACEAE - WATERLEAF FAMILY

Phacelia crenulata Torr.
Headquarters area, BFH 11244, 8 May 1948; Courthouse Wash, LMP 71, 2 May 1963; Win-

dows-Balanced Rock area, LMP 48, 2 May 1963. Locally common.

Phacelia ivesiana Torr.
Courthouse Wash, LBB 66, 2 May 1963; Fiery Furnace, WM 2016, 4 June 1963. Locally abundant.

JUNCACEAE - RUSH FAMILY

Juncus balticus Willd. Rush
Courthouse Wash, GLP 67, 2 May 1963; Salt Wash, near Turnbow Cabin, WHM 2290, 3 August 1963. Common along moist stream courses.

Juncus longistylis Torr.
Freshwater Canyon, WHM 2305, 3 August 1963. Locally abundant.

Juncus saximontanus A. Nels. fma. *brunescens* (Rydb.) Herm.
Freshwater Canyon, WHM 2321, 3 August 1963.

JUNCAGINACEAE - ARROW-GRASS FAMILY

Triglochin maritima L. Arrow-grass
Saltgrass meadow, east of Turnbow Cabin, WM 2033, 4 June 1963.

LABIATAE - MINT FAMILY

Hedeoma drummondii Benth.
Hanging garden, east of Turnbow Cabin, WM 2040, 4 June 1963. Locally common around the hanging gardens.

Poliomintha incana (Torr.) A. Gray Purple sage
Trail to Landscape Arch, BFH 12006, 25 June 1952; Courthouse Wash, LMP 78, 2 May 1963; two miles west of Turnbow Cabin, BFH 11405, 18 May 1949; Headquarters area, WM 1980, 3 June 1963. This plant, immortalized in Zane Grey's "Riders of the Purple Sage," is a dominant species in the communities which occupy the partially stablized dune sands in Arches.

LEGUMINOSAE - PEA FAMILY

Astragalus amphioxys A. Gray Milkvetch
Road to Devil's Garden, WM 1901, 2 May 1963; Windows-Balanced Rock area, WM 1910, 2 May 1963. Common throughout the Monument.

Astragalus ceramicus Sheld.
Landscape Arch, BFH 11416, 19 May 1949; WM 2024, 4 June 1963. Rare; a sand inhabiting milkvetch with bladdery legumes which resemble birds' eggs.

Astragalus coltonii M. E. Jones var. *moabensis* M. E. Jones
Fiery Furnace, BFH 11136, 25 April 1947; Road to Devil's Garden, WM 1902, 2 May 1963. Uncommon; a handsome tall species with racemes of bright pink-purple flowers.

Astragalus cymboides M. E. Jones
Turnbow Cabin, BFH 11399, 18 May 1949.

Astragalus desperatus M. E. Jones
Turnbow Cabin, 11154, 27 April 1947; Courthouse Towers, BFH 11242, 8 May 1948; Windows-Balanced Rock area, WM 1911, 2 May 1963. This interesting small milkvetch is uncommon in the Monument proper, but is common along the Colorado River.

Astragalus flavus Nutt.
Road to Turnbow Cabin, Mancos shale formation, WM 1905, 2 May 1963. Known only from the collection site. The plant is an indicator of selenium.

Astragalus lentiginosus Dougl. var. *palans* (M. E. Jones) M. E. Jones
Windows-Balanced Rock area, WM 1908, 2 May 1963; Headquarters area, BFH 25 April 1947; Courthouse Towers, BFH 11383, 17 May 1949. Common along roadsides throughout the region.

Astragalus mollissimus Torr. var. *thompsonae* (S. Wats.) Barneby
Fiery Furnace, BFH 11138, 26 April 1947; Windows-Balanced Rock area, BFH 11263, 9 May 1948; WM 1909, 2 May 1963. Widely distributed throughout sandy areas of the Monument but seldom common.

Astragalus praelongus Sheld.
One mile west of Turnbow Cabin, BFH 11406, 18 May 1949; Road to Devil's Garden, WM 1904, 2 May 1963. An indicator of seleniferous soils; locally abundant on alluvium and on the Paradox formation in Salt Valley.

Astragalus preussii A. Gray
Courthouse Towers, BFH 11125, 25 April 1947; Courthouse Wash, WM 1912, 2 May 1963. Locally common along roadsides in the southern part of the Monument.

Glycyrrhiza lepidota Pursh Wild licorice
Freshwater Canyon, WHM 2327, 3 August 1963; WHM 2344, 4 August 1963. Uncommon.

Lupinus argenteus Pursh
Landscape Arch, BFH 11414, 19 May 1949. WM 2028, 1 June 1963. Rare.

Lupinus pusillus Pursh
Headquarters area, BFH 11367, 17 May 1949, Courthouse Towers, BFH 11243, 8 May 1948. Landscape Arch, WM 1906, 2 May 1963. Locally abundant in sandy areas.

Melilotus alba Desr. ex Lam. White sweetclover
Salt Wash, near Turnbow Cabin, WHM 2287, 3 August 1963. Adventive forage plant; uncommon.

Melilotus officinalis (L.) Lam. Yellow sweetclover
Freshwater Canyon, WM 3015, 4 June 1964. Adventive forage plant.

Petalostemon flavescens S. Wats Prairie clover
Alluvium, Salt Valley near Fiery Furnace, WM 2004, 4 June 1963. Abundant at this location; otherwise not noted.

Petalostemon occidentale (Heller) Fern.
Below Delicate Arch, BFH 12019, 26 May 1952; Headquarters area, WM 1987. The common prairie clover in the Monument; widely distributed and common locally.

Psoralea lanceolata Pursh Scurf-pea
Headquarters area, BFH 11367, 17 May 1949, Landscape Arch, WM 2027, 4 June 1963. Rare.

Robinia pseudoacacia L. Black locust
Headquarters area, WM 1996, 3 June 1963. Cultivated ornamental from the eastern United States.

Sophora stenophylla A. Gray
Arches National Monument, Richards s.n., 11 May 1963. Rare.

LILIACEAE - LILY FAMILY

Allium textile Nels. & Macbr. Wild onion
Road to Devil's Garden, LBB 53, 2 May 1963; Courthouse Wash, GLP s. n., 2 May 1963. Locally common in sandy areas of the Monument.

Androstephium breviflorum S. Wats.
Windows-Balanced Rock area, GLP 31, 2 May 1963. Rare.

Asparagus officinalis L.
Courthouse Wash, WM 2828, 30 May 1964. Escaped from cultivation.

Calochortus nuttallii T. & G. Sego lily
Headquarters area, BFH 11370, 17 May 1949, Klondike Wash, WM 2051, 4 June 1963. Widely distributed, uncommon. State flower of Utah.

Smilacina stellata (L.) Desf. False solomonseal
Hanging garden, near Turnbow Cabin, GLP 41, 2 May 1963. Common on the lip of some of the hanging gardens.

Yucca harrimaniae Trel. Yucca
Landscape Arch, BFH 11415, 19 May 1949; Trail to Delicate Arch, Welsh 1920, 11 May 1963. Widely distributed in the Monument.

Zygadenus elegans Pursh Death camas
Hanging garden, north of trail to Delicate Arch, WHM 2335, 4 August 1963. A dominant species in the hanging garden communities, both on the vertical faces and on the lip of the garden.

LINACEAE - FLAX FAMILY

Linum aristatum Engelm. Yellow flax
Summerville formation, near Fiery Furnace, WM 2012, 4 June 1963; stabilized dunes, vicinity of Landscape Arch, WM 2767, 29 September 1963. Common in the latter locality.

LOASACEAE - LOASA FAMILY

Mentzelia multiflora (Nutt.) A. Gray Blazing star
Turnbow Cabin, BFH 11397, 18 May 1949.

Mentzelia pterosperma Eastw.
Courthouse Wash, LMP 75, 2 May 1963.

Mentzelia pumila (Nutt.) T. & G.
Headquarters area, WM 1982, 3 June 1963. Abundant in the sandy flats around headquarters.

MALVACEAE - MALLOW FAMILY

Sphaeralcea coccinea (Pursh) Britt. Globe mallow
Turnbow Cabin, BFH 11152, 27 April 1947; Road to Devil's Garden, LMP 58, 2 May 1963.

Sphaeralcea leptophylla (A. Gray) Rydb.
Summerville formation, near Fiery Furnace, WM 2011, 4 June 1963. Rare.

Sphaeralcea parvifolia A. Nels.
Trail to Landscape Arch, BFH 12003, 25 June 1952; Headquarters area, WM 1915, 3 May 1963.

MORACEAE - MULBERRY FAMILY

Morus alba L. White mulberry
Headquarters area, WM 3014, 4 June 1964. Cultivated ornamental.

Morus rubra L. Red mulberry
Headquarters area, WM 1999, 3 June 1963. Cultivated ornamental.

NYCTAGINACEAE - FOUR O'CLOCK FAMILY

Abronia fragrans Nutt. ex Hook. Sand verbena
Landscape Arch, BFH 11139, 26 April 1947; LMP 63, 2 May 1963; Windows-Balanced Rock area, GLP 27, 2 May 1963. Locally abundant in sandy areas; the flowers are white and very fragrant.

Mirabilis multiflora (Torr.) A. Gray
Freshwater Canyon, WM 3016, 4 June 1964. Rare.

Oxybaphus linearis (Pursh) Robins.
Headquarters area, WM 1977, 3 June 1963.

Tripterocalyx pedunculatus (Jones) Standl.
Courthouse Wash, WM 2819, 30 May 1964.

OLEACEAE - OLIVE FAMILY

Fraxinus anomala Torr. Single-leaf ash
Courthouse Wash, BFH 11127a, 25 April 1947; Windows-Balanced Rock area, LMP 42, 2 May 1963. Common throughout the juniper-pinyon community.

ONAGRACEAE - EVENING PRIMROSE FAMILY

Epilobium adenocaulon Hauskn.
Freshwater Canyon, WHM 2318, 3 August 1963.

Gaura parviflora Dougl.
Courthouse Wash, WM 2814, 30 May 1964.

Oenothera caespitosa Nutt. Evening primrose
Windows-Balanced Rock area, BFH 11262, 9 May 1949; LMP 47, 2 May 1963; Road to Devil's Garden, LMP 59, 2 May 1963. The large white flowers of this species are among the most beautiful in the Monument; widely distributed, common.

Oenothera longissima Rydb.
Hanging garden, north of trail to Delicate Arch, WHM 2332, 4 August 1963. Uncommon; restricted to the lip of the hanging gardens.

Oenothera pallida (Lindl.) Britt.
Headquarters area, BFH 11246, 8 May 1948; Courthouse Towers, BFH 11382, 17 May 1949; Landscape Arch, LMP 67, 2 May 1963. Common to locally abundant in sandy areas. This species turns the headquarters area into a veritable flower garden during early May.

ORCHIDACEAE - ORCHID FAMILY

Epipactis gigantea Dougl. Helleborine
Hanging garden, one mile east of Turnbow Cabin, BFH 11254, 8 May 1948; do 11401, 18 May 1948; WM 2038, 4 June 1963; Four miles northeast of Windows area, BFH 12013, 25 June 1952. Common; lip of hanging gardens.

Habenaria sparsiflora S. Wats. Bog orchid
Hanging garden, east side of Salt Wash Canyon, WM 2735, 28 September 1963. Rare.

OROBANCHACEAE - BROOM-RAPE FAMILY

Orobanche fasciculata Nutt. Cancer-root
Landscape Arch, WM 2023, 4 June 1963. Rare.

PINACEAE - PINE FAMILY

Juniperus osteosperma (Torr.) Little Utah juniper
Courthouse Wash, LMP 73, 2 May 1963. Dominant evergreen tree in the juniper-pinyon community.

Pinus edulis Engelm. Pinyon pine
Devil's Garden, LMP 60, 2 May 1963. Less abundant in the pinyon-juniper community than Utah juniper.

PLANTAGINACEAE - PLANTAIN FAMILY

Plantago purshii R. & S.
Windows-Balanced Rock area, LMP, 2 May 1963. Locally abundant in sandy soils.

POLEMONIACEAE - PHLOX FAMILY

Gilia congesta Hook.
Headquarters area, WM 1995, 3 June 1963. Rare.

Gilia gunnisonii T. & G.
Headquarters area, WM 1983, 3 June 1963. Locally abundant in sandy soils.

Gilia leptomeria A. Gray
Headquarters area, BFH 11248, 8 May 1948; Road to Devil's Garden, LMP 57, 2 May 1963.

Leptodactylon watsonii (A. Gray) Rydb.
Windows area, BFH 11396, 18 May 1949. Cliff base, north of trail to Delicate Arch, WHM 2340, 4 August 1963. Locally common, forming hemispheric clumps.

POLYGALACEAE - MILKWORT FAMILY

Polygala subspinosa S. Wats.
Freshwater Canyon, WHM 2306, 3 August 1963. Rare.

POLYGONACEAE - BUCKWHEAT FAMILY

Eriogonum alatum Torr.
Trail to Delicate Arch, BFH 12016, 26 June 1952; WM 2046, 4 June 1963. Uncommon on the Navajo Sandstone in the vicinity of the trail to Delicate Arch.

Eriogonum bicolor M. E. Jones
Turnbow Cabin vicinity, BFH 11149, 27 April 1947; do 11409, 18 May 1949; Road to Devil's Garden, GLP 49, 2 May 1963. Locally common, especially on clay soils.

Eriogonum corymbosum Benth.
Mancos shale formation, near Turnbow Cabin, WM 2709, 28 September 1963. Common in this locality.

Eriogonum divergens Small
Courthouse Towers, WHM 2260, 3 August 1963. Common in the Courthouse Towers area, where it forms large hemispheric shrubs two to four feet in diameter. When in flower the plants appear as large whitish mounds.

Eriogonum gordonii Benth.
Courthouse Wash, LBB 67, 2 May 1963. This is the most common annual *Eriogonum* in the Monument. During late summer and autumn the plants line the roadsides.

Eriogonum inflatum Torr. & Frem.
Road to Devil's Garden, GLP 47, 2 May 1963; Courthouse Towers, WHM 2260, 3 August 1963. Locally common, especially on heavier soils.

Eriogonum microthecum Nutt.
Headquarters area, WM 1993, 3 June 1963; Salt Wash, slick rock on east side, WM 2733, 28 September 1963. Widely distributed on the sandstone formations in the Monument.

Eriogonum sp.
Courthouse Towers, WHM 2265, 3 August 1963. Common in the sandy regions of the Monument.

Rumex hymenosepalus Torr. Dock
Headquarters area, BFH 11249, 8 May 1948. Landscape Arch, LBB 61, 2 May 1963; Balanced Rock area, LBB 32, 2 May 1963. Common in the sandy regions of the Monument.

POLYPODIACEAE - FERN FAMILY

Adiantum capillus-veneris L. Maidenhair fern
Hanging garden, west of Turnbow Cabin, BFH 11145, 27 April 1947; GLP 41, 2 May 1963. A dominant species in the hanging gardens of the region.

Cystopteris fragilis (L.) Bernh.
Freshwater Canyon, WHM 2320, 3 August 1963. Uncommon.

Pellaea breweri D. C. Eaton Cliffbrake
Cliff face, north of trail to Delicate Arch, WHM 2341, 4 August 1963. Rare.

Pellaea limitanea (Maxon) Morton
Cliff base, lower Courthouse Wash, WM 2757, 28 September 1963. Rare.

Pteridium aquilinum (L.) Kuhn. Bracken
Hanging garden, Freshwater Canyon, LMP 54, 2 May 1963. Uncommon.

PORTULACACEAE - PURSLANE FAMILY

Portulaca oleracea L. Purslane
Turnbow Cabin, Moore 41, 8 September 1963. Locally abundant, adventive.

PRIMULACEAE - PRIMROSE FAMILY

Primula specuicola Rydb. Easter flower
Hanging garden, near Turnbow Cabin, BFH 11141, 27 April 1947; LBB 50, 2 May 1963. Endemic to hanging gardens in southern Utah and northern Arizona. This species occupies that part of the hanging garden immediately below the scarlet monkey flower, although it is sometimes mixed with other species at the base of the vertical wall.

RANUNCULACEAE - BUTTERCUP FAMILY

Aquilegia micrantha Eastw. Columbine
Hanging garden, near Turnbow Cabin, BFH 11142, 25 April 1947; do 11256, 8 May 1948; do 11400, 18 May 1949; GLP 45, 2 May 1963. A dominant species on the lip of the hanging gardens; common.

Clematis ligusticifolia Nutt. ex T. & G. Virgin's bower
Fiery Furnace, WM 2014a, 4 June 1963; Freshwater Canyon, WHM 2322, 3 August 1963. Uncommon.

Delphinium scaposum Greene
Courthouse Towers, BFH 11380, 17 May 1949; Windows area, Welsh 1924, 11 May 1963. Uncommon.

RHAMNACEAE - BUCKTHORN FAMILY

Rhamnus betulaefolia Greene Buckthorn
Lower Courthouse Wash, WM 2760, 28 September 1963. Uncommon; rocky canyon sides.

ROSACEAE - ROSE FAMILY

Amelanchier utahensis Koehne Utah serviceberry
Near Turnbow Cabin, BFH 11147, 27 April 1947; Courthouse Towers, BFH 11379, 17 May 1949; Landscape Arch, LBB 58, 2 May 1963; Windows-Balanced Rock area, LBB 36, 2 May 1963. Widespread but uncommon.

Cercocarpus intricatus S. Wats Mountain mahogany
Delicate Arch, BFH 11259, 8 May 1948; Windows-Balanced Rock area, LMP 39, 2 May 1963. Common in shallow soils on sandstone formations.

Cercocarpus montanus Raf.
Windows area, BFH 11134, 25 April 1947; do 11260, 8 May 1948; Courthouse Wash, GLP 58, 2 May 1963; Windows-Balanced Rock area, LBB 38, 2 May 1963. Widespread in the Monument.

Coleogyne ramosissima Torr. Blackbrush
Headquarters area, BFH 11122, 25 April 1947; Courthouse Towers, BFH 11384, 17 May 1949; Courthouse Wash, LBB 64, 2 May 1963; Windows-Balanced Rock area, LMP 45, 2 May 1963. A dominant species over much of the sandy well-drained soils in the Monument.

Cowania mexicana D. Don Cliffrose
Courthouse Wash, LMP 69, 2 May 1963; Windows-Balanced Rock area, LBB 39, 2 May 1963. Widespread in the Monument and locally common.

Rosa woodsii Lindl. Wild rose
Freshwater Canyon, WHM 2309, 3 August 1963. Uncommon.

Spiraea caespitosa Nutt.
Courthouse Wash, WM 2829, 30 May 1964.

RUBIACEAE - MADDER FAMILY

Galium coloradoense W. F. Wright Bedstraw
Salt Wash, WM 2741, 28 September 1963.

Galium triflorum Michx.
Freshwater Canyon, WHM 2319, 3 August 1963.

SALICACEAE - WILLOW FAMILY

Populus alba L. White poplar
Cultivated, Headquarters area, WM 1997, 3 June 1963.

X *Populus canadensis* Moench. Carolina poplar
Headquarters area, WM 2747, 28 September 1963. Cultivated ornamental around Visitor Center; a hybrid between *P. deltoides* and *P. nigra*.

Populus fremontii S. Wats. Fremont poplar
Courthouse Towers, BFH 11162, 27 April 1947; Courthouse Wash, LBB 68, 2 May 1963; Base of cliff north of trail to Delicate Arch, WHM 2339, 4 August 1963. Uncommon; restricted to moist areas such as water courses.

Salix amygdaloides Anderss. Peachleaf willow
Courthouse Wash, LBB 70, 2 May 1963; Freshwater Canyon, WHM 2310, 3 August 1963. Quite common along streamcourses in the area; occasionally reaches a height of twenty feet.

Salix lutea Nutt. Willow
Hanging garden, west of Turnbow Cabin, LBB 47, 2 May 1963. Uncommon.

SANTALACEAE - SANDALWOOD FAMILY

Comandra umbellata (L.) Nutt. Bastard toadflax
Windows area, BFH 11132, 25 April 1947; Courthouse Towers, BFH 11375, 17 May 1949; Courthouse Wash, LBB 63, 2 May 1963; Windows-Balanced Rock area, LBB 31, 2 May 1963. Widely distributed; common.

SAXIFRAGACEAE - SAXIFRAGE FAMILY

Fendlera rupicola A. Gray Fendlerbrush
Lower Courthouse Wash, WM 2752, 28 September 1963. Uncommon.

SCROPHULARIACEAE - FIGWORT FAMILY

Castilleja chromosa A. Nels. Indian paintbrush
Windows area, BFH 11131, 25 April 1947; do 11391, 18 May 1949; Courthouse Towers,

BFH 11238, 7 May 1948, two miles west of Turnbow Cabin, BFH 11407, 18 May 1949; Windows-Balanced Rock area, LMP 49, 2 May 1963, near Turnbow Cabin, GLP 40, 2 May 1963. Widely distributed in the monument but not really common. The bright red flowers stand out sharply in the early spring flora.

Castilleja linariaefolia Benth.

Windows area, BFH 11160, 27 April 1947; Hanging Garden, near Turnbow Cabin, WM 2039, 4 June 1963. Locally common in the vicinity of the hanging gardens.

Cordylanthus wrightii A. Gray ex. Torr.

Courthouse Towers, WM 2262, 3 August 1963. Uncommon.

Linaria dalmatica (L.) Mill.

Headquarters area, WM 2804, 29 May 1964. Adventive ornamental.

Mimulus eastwoodiae Rydb.

Scarlet monkeyflower

Hanging garden, east of Turnbow Cabin, WM 2037, 4 June 1963; Freshwater Canyon, WHM 2323, 3 August 1963. A dominant species in the hanging gardens of the region. They occupy the uppermost vegetative stratum in the gardens.

Penstemon cyanocaulis Payson

Windows-Balanced Rock area, WM 1907, 2 May 1963. A blue-flowered species; rare.

Penstemon eatonii A. Gray

Courthouse Wash, LMP 72, 2 May 1963; Courthouse Towers, BFH 11241, 8 May 1948. This *Penstemon*, with the bright red, tubular flowers, is one of the most striking of all flowering plants in the Monument; uncommon.

Penstemon utahensis Eastw.

Windows area, BFH 11158, 27 April 1947; Near Turnbow Cabin, LMP 50, 2 May 1963. Rare; a red-flowered plant of low stature which differs from the above species in having trumpet-shaped flowers with a spreading limb.

SOLANACEAE - NIGHTSHADE FAMILY

Physalis fendleri A. Gray

Courthouse Wash, WM 2815, 30 May 1964.

TAMARICACEAE - TAMARISK FAMILY

Tamarix pentandra Pall. Tamarisk

Courthouse Wash, GLP 64, 2 May 1963; Salt Wash, north of Freshwater Canyon, WM 2729, 28 September 1963. Adventive from Europe and becoming widely distributed during the past thirty years (Christensen, 1962).

ULMACEAE - ELM FAMILY

Celtis reticulata Torr. Native hackberry

Trail to Delicate Arch, WM 2045, 4 June 1963. Uncommon; usually occurring as dwarf twisted specimens which have very rough, insect-infested leaves.

Ulmus pumila L. Siberian elm

Headquarters area, WM 2746, 28 September 1963. Cultivated ornamental from the Old World.

UMBELLIFERAE - CARROT FAMILY

Cymopterus newberryi (S. Wats.) M. E. Jones

Road to Devil's Garden, LBB 52, 2 May 1963; Headquarters area, BFH 11245, 8 May 1948. Uncommon but widely distributed.

Lomatium latilobum (Rydb.) Mathias

Biscuit root

Windows area, BFH 11133, 25 April 1947; Fiery Furnace, BFH 11137, 26 April 1947; Trail to Landscape Arch, GLP 51, 2 May 1963. Common between the great sandstone fins in Devil's Garden and in the Fiery Furnace where the plants occur in great mounds, some to three feet in diameter.

Lomatium parryi (S. Wats.) M. E. Jones

Courthouse Towers, BFH 11372, 17 May 1949; Landscape Arch, LMP 61, 2 May 1963; Windows-Balanced Rock area, LBB 35, 2 May 1963. Widely distributed in sandy soils in the juniper-pinyon community; uncommon.

TYPHACEAE - CATTAIL FAMILY

Typha latifolia L. Cattail

Salt Wash, near Turnbow Cabin, WHM 2280, 3 August 1963. Uncommon; the fruiting inflorescenses of the specimens collected are among the largest examined.

ZYGOPHYLLACEAE - CALTROP FAMILY

Tribulus terrestris L. Puncture vine

Headquarters area, WM 2532, 18 August 1963. Common along roadsides in the headquarters area; an introduced weed.

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ARTHROPOD ASSOCIATES OF PLANTS AT THE NEVADA TEST SITE

by

DORALD M. ALLRED AND D ELDEN BECK

BIOLOGICAL SERIES — VOLUME V, NUMBER 2

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FOREWORD

This is another of a series of major publications on desert ecology resulting from studies at the Nevada Test Site by the Brigham Young University Department of Zoology and Entomology in cooperation with the United States Atomic Energy Commission. Although some of the studies are the result of independent investigations by specialists who are not on our departmental staff, they are part of the major project initiated cooperatively by B.Y.U. and the A.E.C. to determine the effect of nuclear detonations on the native animals of the Nevada Test Site.

Dorald M. Allred and
D Elden Beck
Project Supervisors

TABLE OF CONTENTS

	Page
INTRODUCTION	1
METHODS	1
ARTHROPOD ASSOCIATES	5
Pseudoscorpions (Pseudoscorpionida)	5
Spiders (Araneida)	5
Mites (Acarina)	6
Spring-tails (Collembola)	7
Psocids (Psocoptera)	7
Thrips (Thysanoptera)	7
Bugs (Hemiptera)	7
Aphids, Scale Insects and Relatives (Homoptera)	7
Nerve-Winged Insects (Neuroptera)	7
Butterflies and Moths (Lepidoptera)	7
Beetles (Coleoptera)	7
Ants, Bees, Wasps, and Relatives (Hymenoptera)	8
Flies (Diptera)	8
DISCUSSION	8
LITERATURE CITED	8

LIST OF TABLES AND FIGURES

Table

	Page
1. Plant community and specific localities of plant collections at the Nevada Test Site	5
2. Relative numbers of arthropods of orders and families associated with each plant species	6

Figure

1. Plant of *Larrea divaricata* showing protective canvas	2
2. Process of cutting plant for transport to the laboratory	3
3. Bottle used to measure volume of base and roots of plant, and humus on ground	4
4. Berlese funnel used for extraction of arthropods	5
5. Relative abundance of arthropods associated with *Atriplex canescens*	9
6. Relative abundance of arthropods associated with *Atriplex confertifolia*	9
7. Relative abundance of arthropods associated with *Coleogyne ramosissima*	9
8. Relative abundance of arthropods associated with *Eurotia lanata*	9
9. Relative abundance of arthropods associated with *Grayia spinosa*	10
10. Relative abundance of arthropods associated with *Kochia americana*	10
11. Relative abundance of arthropods associated with *Larrea divaricata*	10
12. Relative abundance of arthropods associated with *Lycium andersoni*	10
13. Relative abundance of arthropods associated with *Lycium pallidum*	11
14. Relative abundance of arthropods associated with *Salsola kali*	11
15. Relative abundance of arthropods associated with *Yucca brevifolia*	11
16. Seasonal occurrence of Homoptera and Thysanoptera on *Atriplex canescens*	11
17. Seasonal occurrence of Diptera and Hemiptera on *Atriplex canescens*	12
18. Seasonal occurrence of Coleoptera and Acarina on *Atriplex canescens*	12
19. Seasonal occurrence of Lepidoptera and Hemiptera on *Atriplex confertifolia*	12
20. Seasonal occurrence of Acarina and Hymenoptera on *Atriplex confertifolia*	12
21. Seasonal occurrence of Diptera and Homoptera on *Atriplex confertifolia*	12
22. Seasonal occurrence of Thysanoptera and Collembola on *Coleogyne ramosissima*	12
23. Seasonal occurrence of Acarina and Homoptera on *Coleogyne ramosissima*	13
24. Seasonal occurrence of Coleoptera and Hymenoptera on *Coleogyne ramosissima*	13
25. Seasonal occurrence of Diptera on *Coleogyne ramosissima*	13
26. Seasonal occurrence of Hemiptera on *Eurotia lanata*	13
27. Seasonal occurrence of Collembola and Thysanoptera on *Eurotia lanata*	13
28. Seasonal occurrence of Homoptera and Acarina on *Eurotia lanata*	13
29. Seasonal occurrence of Diptera and Coleoptera on *Grayia spinosa*	14
30. Seasonal occurrence of Thysanoptera and Homoptera on *Grayia spinosa*	14
31. Seasonal occurrence of Collembola and Hemiptera on *Grayia spinosa*	14
32. Seasonal occurrence of Acarina on *Grayia spinosa*	14
33. Seasonal occurrence of Acarina and Homoptera on *Kochia americana*	14
34. Seasonal occurrence of Collembola and Thysanoptera on *Kochia americana*	14

35. Seasonal occurrence of Coleoptera and Hemiptera on *Kochia americana* 15
36. Seasonal occurrence of Acarina and Thysanoptera on *Larrea divaricata* 15
37. Seasonal occurrence of Coleoptera and Hymenoptera on *Larrea divaricata* 15
38. Seasonal occurrence of Coleoptera and Diptera on *Lycium andersoni* 15
39. Seasonal occurrence of Lepidoptera and Thysanoptera on *Lycium andersoni* 15
40. Seasonal occurrence of Acarina and Homoptera on *Lycium andersoni* 15
41. Seasonal occurrence of Lepidoptera and Thysanoptera on *Lycium pallidum* 16
42. Seasonal occurrence of Homoptera and Coleoptera on *Lycium pallidum* 16
43. Seasonal occurrence of Acarina on *Lycium pallidum* 16
44. Seasonal occurrence of Hemiptera on *Salsola kali* 16
45. Seasonal occurrence of Acarina and Homoptera on *Yucca brevifolia* 16
46. Seasonal occurrence of Diptera and Coleoptera on *Yucca brevifolia* 16

ARTHROPOD ASSOCIATES OF PLANTS AT THE NEVADA TEST SITE*

By

Dorald M. Allred and D Elden Beck**

INTRODUCTION

This study was made to determine plant-arthropod associations related to the predominant plants in several plant communities at the Nevada Test Site. In our arthropod studies, special emphasis has been directed to the identification of kinds, relative numbers, seasonal incidence and ecological distribution relative to the plant communities as well as individual plant species. These data contribute to the over-all objectives of the ecological studies being conducted by the Brigham Young University Zoology and Entomology Department in cooperation with the U. S. Atomic Energy Commission. These objectives and community designations were reported by Allred, Beck and Jorgensen (1963a).

Ideally the arthropods in this study should have been discussed at the species level. Due to difficulty in obtaining help from taxonomic specialists this was not possible, and we used only the higher taxonomic categories. Nevertheless, we feel that groups of species with similar anatomical, physiological and ecological characteristics may be dealt with collectively. This will provide a basis for further studies on the species level by specialists trained to study such organisms.

In our ecological studies we have collected and preserved thousands of arthropods. Detailed ecological data for each have been recorded. Although some of these organisms may never be studied at the species level, it is expected that most eventually will be so studied and thus vindicate the original effort of making the collections.

METHODS

Plants of eleven species were studied. Each month one plant of each species was taken from a specific area in one of the biotic communities. (For the location of these areas see Table 1.) Each individual plant that was selected was not immediately adjacent to a different species but more or less stood alone.

The following technique was used for each collection. A white canvas cloth was placed on the ground around the plant, snuggly fitting about the base at ground contact (Fig. 1). This was done to collect organisms as they fell from the plant while it was being examined and thus avoid soil and humus contamination by the stem- and leaf-dwelling arthropods. Next was the systematic removal of stems and leaves. These were cut by hand clippers and placed into paper bags (Fig. 2). Specimens and plant debris falling onto the cloth were also placed into the bag containing the stems and leaves. The canvas was then removed, and the surface soil and humus plus the base of the plant and large roots were collected, measured volumetrically and placed in a second bag (Fig. 3). The bags were taken to the laboratory and their contents placed in separate Berlese funnels 18 inches in diameter and 3 feet long (Fig. 4). The funnels were operated for 24 to 36 hours for each collection. Specimens were collected in catch-bottles containing 70 percent alcohol. Specimens in each bottle were sorted to the taxonomic division of Order, and in a few cases the Family. The number of each kind was then determined.

Inasmuch as individual plants varied in size, and the amount of soil and humus taken also varied from plant to plant, corrections for the different volumes were made so that figures used for population analysis would be on a comparative basis. For example, if the total number of arthropods taken from the largest volume of a single plant was 100, then a number of 5 taken from only one-tenth the volume with reference to a different plant was adjusted to 50.

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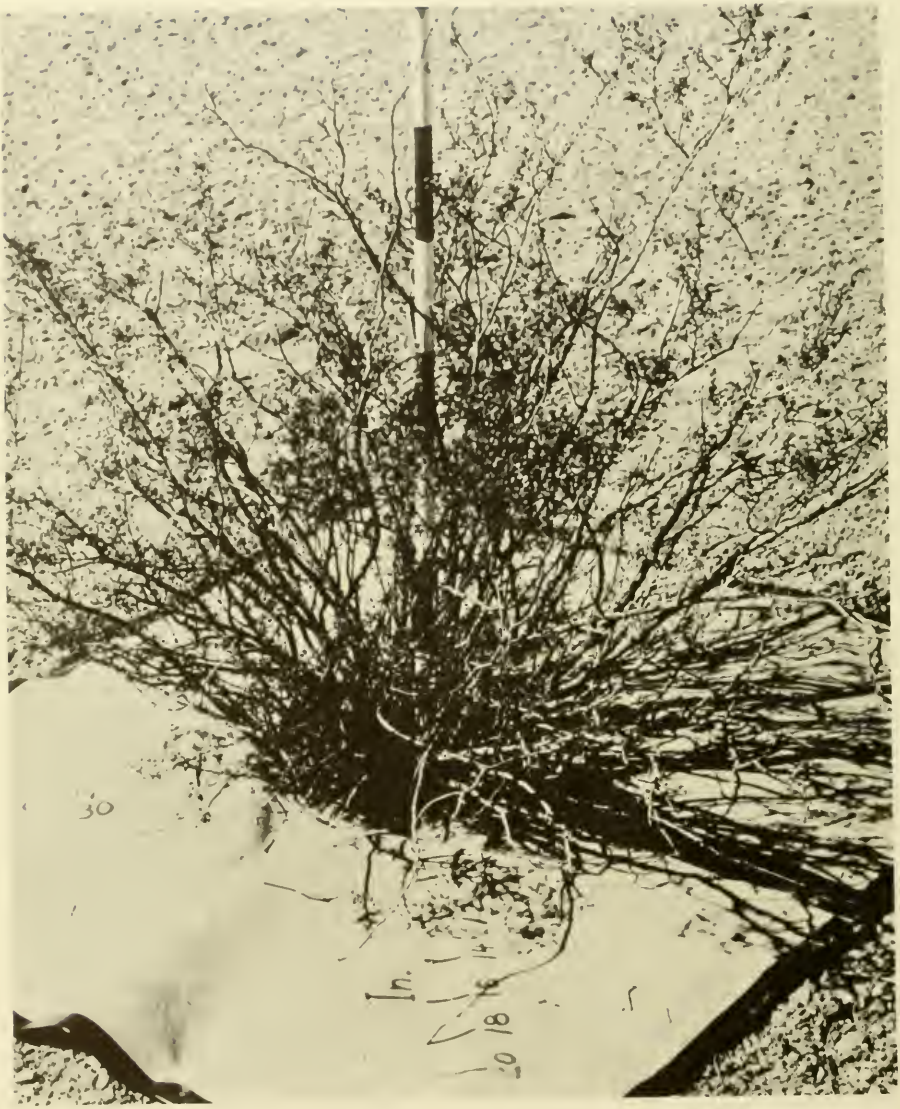

Figure 1. Plant of *Larrea divaricata* showing protective canvas.

Figure 2. Process of cutting plant for transport to the laboratory.

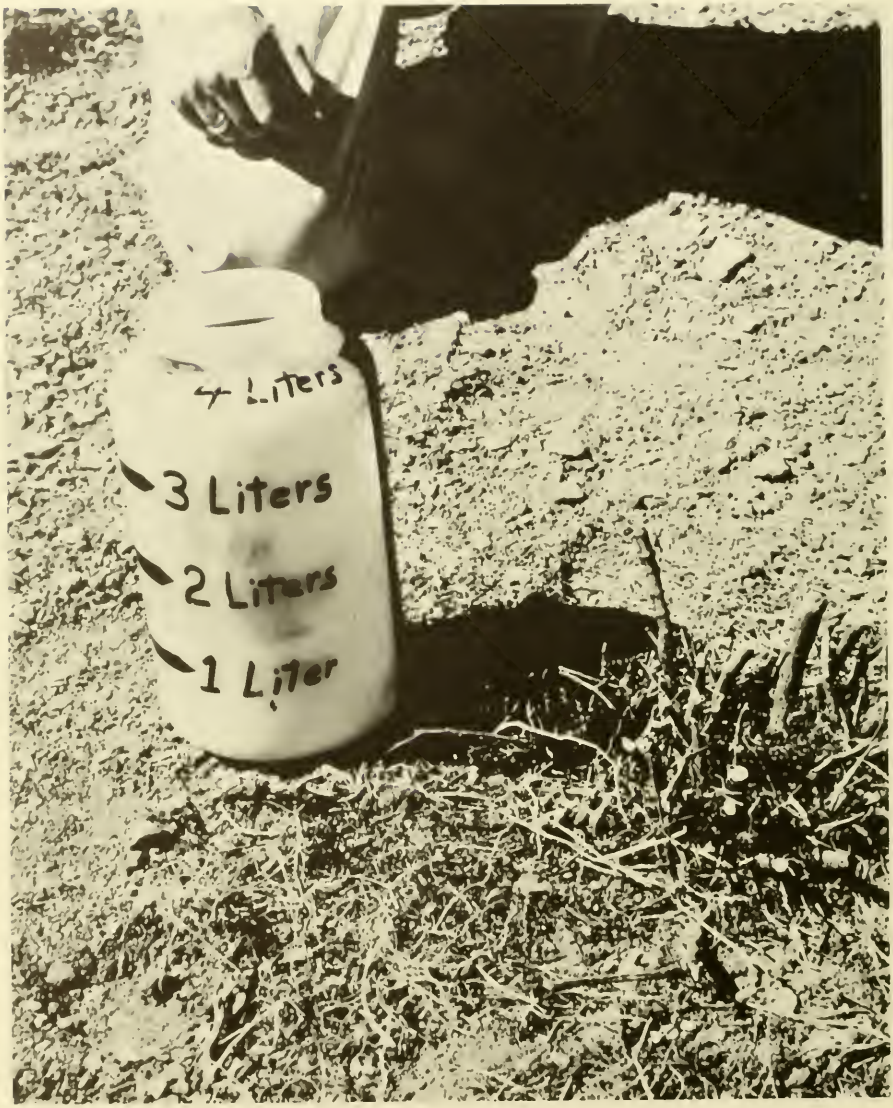

Figure 3. Bottle used to measure volume of base and roots of plant, and humus on ground.

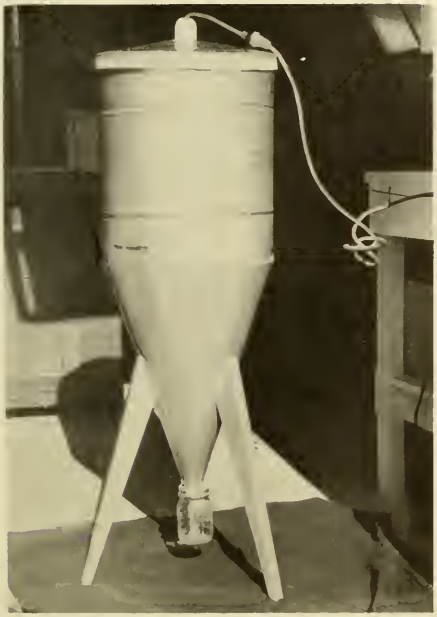

Figure 4. Berlese funnel used for extraction of arthropods.

ARTHROPOD ASSOCIATES

Relative numbers of individuals of each order and some families with their plant associations are shown in Table 2. Figures 5 to 15 show the relative abundance of arthropods on the stems and leaves as compared with the numbers in the soil and humus of each plant. Figures 16 to 46 show the seasonal occurrence of the predominant groups of arthropods relative to each plant species.

Pseudoscorpions
(Pseudoscorpionida)
Figs. 5-15

These arachnids were most commonly associated with *Atriplex confertifolia*, but were also found with *Coleogyne ramosissima*, *Larrea divaricata* and *Lycium* spp. All were taken from the soil and humus. The minimal amounts of moist decaying organic debris under the plants likely is a critical factor affecting the presence of these organisms.

Spiders
(Araneida)
Figs. 5-15

Although not in great numbers, spiders were found associated with all plant species except *Salsola*. They were least abundant with *Kochia*,

Table 1. Plant community and specific localities* of plant collections at the Nevada Test Site.

Atriplex canescens (*Grayia-Lycium* Community, Study 6 D D) - 3.2 miles S of Well 3 B.

Atriplex confertifolia (*Atriplex-Kochia* Community, Study 6 D A) - 0.5 mile S of Well 3 B, thence 0.6 mile E.

Coleogyne ramosissima (*Coleogyne* Community, Study 2 D A) - 11 miles N of Well 3 B on Rainier Mesa road, thence 100 yards S.

Eurotia lanata (*Grayia-Lycium* Community, Study 6 D C) - Environs of Well 3 B.

Grayia spinosa (*Grayia-Lycium* Community, Study 4 D A) - 4.2 miles N of Well 3 B along Rainier Mesa Road, thence 1 mile W.

Kochia americana (*Atriplex-Kochia* Community, Study 6 D B) - 0.5 mile S of Well 3 B, thence 0.6 mile E.

Larrea divaricata (*Larrea-Franseria* Community, Study 5 D A) - 0.3 mile E of Mercury Highway, N of Well 5 B road.

Lycium andersoni (*Grayia-Lycium* Community, Study 4 D B) - 4.2 miles N of Well 3 B along Rainier Mesa Road thence 1 mile W.

Lycium pallidum (*Larrea-Franseria* Community, Study 5 D B) - 1.1 miles E of Mercury Highway, thence 1 mile S of Well 5 B road.

Salsola kali (*Salsola* Community, Study 1 E A) - 150 yard radius, 1320 ft. SE of GZ-1.

Yucca brevifolia (*Coleogyne* Community, Study 6 D E) 4.7 miles S of Well 3 B.

*For mapped localities of the studies (6 D D, etc.) refer to Allred, Beck and Jorgensen (1963b).

Table 2. Relative numbers of individuals of orders and families of arthropods associated with each plant species.

	Plant										
Arthropod Group	Atr can	Atr con	Col ram	Eur lan	Gra spi	Koc ame	Lar div	Lyc and	Lyc pal	Sal kal	Yuc bre
Pseudoscorpionida		12	5				6	5	1		
Araneida	45	22	14	28	18	3	35	16	13		51
Acarina	951	1025	2164	661	1207	1246	1296	704	473	9	373
Collembola	25	23	556	1251	212	259	60	63	57		17
Psocoptera	28	34	9	16	3	10	106	21	2		
Thysanoptera	650	32	388	1853	90	225	674	97	223		17
Hemiptera											
Corimelaenidae					59			4			
Corizidae							1				
Lygaeidae	6						2			2526	
Miridae	119	81		57	77	20	13	19	8	2	17
Nabidae										1	
Pentatomidae										2	
Tingidae	3			87							
Homoptera											
Aphididae	21	51	14	31	5	4					
Cicadellidae	211	101	57	101	10		19	16			
Coccidae	670	2011	1249	1106	274	2303	233	25	82		631
Fulgoridae			1	21		6					
Membracidae				2	1		819				
Psyllidae								3711	4		
Neuroptera	8	17		5	4						
Lepidoptera	55	139	1	23	29	49	44	213	190		5
Coleoptera	204	42	225	150	286	224	196	112	83		665
Hymenoptera											
Bethylidae										1	
Braconidae				4	1						
Ceraphronidae	3	1			1						
Encyrtidae	9		9	13					4		
Eulophidae				9							
Formicidae	4	208	293	9	53		82	4	35	7	
Mymaridae			8						1		
Pteromalidae	4	1	28	19	4		22	13			17
Sclerogibbidae		1									
Tiphiidae	2			2			1				
Diptera	158	121	116	38	112	3	42	122	57		179

and they were most commonly associated with *Yucca* and *Atriplex canescens*. In association with *Atriplex confertifolia*, *Eurotia* and *Yucca* they were found in about equal abundance on the stems and leaves and in the soil and humus. In other plant associations they were more common in the soil and humus.

Mites
(Acarina)

Figs. 5-15, 18, 20, 23, 28, 32, 33, 36, 40, 43, 45

These animals were associated with all the plant species except *Salsola*. They were most commonly found with *Coleogyne*, but were moderately abundant with *Atriplex confertifolia*, *Grayia*, *Kochia* and *Larrea*. With *Coleogyne*, *Eurotia*, *Kochia*, *Larrea* and *Salsola* they were found predominantly on the stems and leaves. With *Yucca* they were about evenly distributed between stems-leaves and soil-humus. In other plant associations they were more common in the soil and humus. The seasonal population peaks of the mites varied considerably with the plant species. Highest populations were not necessarily more common for one month than another except November when peaks occurred with *Atriplex canescens* and *Kochia*.

Spring-tails
(Collembola)
Figs. 5-15, 22, 27, 31, 34

These insects were most abundantly associated with *Eurotia*. They were not found with *Salsola* and occurred least with *Yucca*. With *Atriplex canescens*, *Coleogyne* and *Kochia* they were found more abundantly on the stems and leaves, whereas with *Grayia* and *Lycium pallidum* they were about evenly distributed between stems-leaves and soil-humus. In other associations they were more common in the soil and humus.

Psocids
(Psocoptera)
Figs. 5-15

Psocids were found in small numbers in association with all plant species except *Salsola* and *Yucca*. They were most abundant with *Larrea* and least with *Grayia* and *Lycium pallidum*. They were more abundant on the stems and leaves of *Grayia*, about evenly distributed between stems-leaves and soil-humus with *Atriplex canescens* and *Coleogyne*, and occurred predominantly in the soil and humus with other plants.

Thrips
(Thysanoptera)
Figs. 5-16, 22, 27, 30, 34, 36, 39, 41

Thysanopterans were associated with every plant species studied except *Salsola*. Their occurrence was infrequent with *Yucca* and *Atriplex confertifolia*, and they were most abundant with *Eurotia*. They were commonly found on the stems and leaves except in association with *Atriplex confertifolia* and *Yucca* where they were predominant in the soil and humus. With *Eurotia* they were about evenly distributed between the two locations. Seasonally, highest populations occurred in April with *Kochia*, *Larrea* and *Lycium* spp., and in June with *Eurotia* and *Grayia*.

Bugs
(Hemiptera)
Figs. 5-15, 17, 19, 26, 31, 35, 44

Hemiptera were found associated with every plant species but were rarely taken in association with *Coleogyne* and *Yucca*. Highest numbers occurred with *Salsola*. Insects of the family Miridae were found with all plants except *Coleogyne*. Large numbers with *Salsola* consisted principally of bugs of the family Lygaeidae. Other families were represented only by small numbers of individuals. With *Lycium* spp. the bugs were about evenly distributed between stems-leaves and soil-humus. With *Coleogyne* and *Salsola* they were predominantly in the soil and humus. With other plants they were principally on the stems and leaves. Highest populations for nymphs occurred in March with *Atriplex* spp. and *Kochia*, and for adults in June with *A. canescens* and *Eurotia*.

Aphids, Scale Insects and Relatives
(Homoptera)
Figs. 5-16, 21, 23, 28, 30, 33, 40, 42, 45

These insects were found in association with all plant species studied. They were infrequently associated with *Salsola* but commonly found with *Lycium andersoni*. The majority taken belonged to the family Coccidae, but insects of the families Cicadellidae and Aphididae were present with more than half of the plants. Psyllids were numerous with *L. andersoni*, but were not found with any other plant except for small numbers with *L. pallidum*. With *L. pallidum* and *Yucca* these insects were about evenly distributed between stems-leaves and soil-humus. With all other plants they were more abundant on stems and leaves. Seasonally April was a month when populations were highest with *Grayia*, *Kochia* and *L. pallidum*. May was the peak month with *Atriplex confertifolia* and *L. andersoni*.

Nerve-Winged Insects
(Neuroptera)
Figs. 5-15

These insects were found in small numbers with only four plants. They were predominant on the stems and leaves with *Eurotia* and *Grayia*, and in the soil and humus with *Atriplex* spp.

Butterflies and Moths
(Lepidoptera)
Figs. 5-15, 19, 39, 41

These animals were associated with every plant except *Salsola*, but only few numbers were taken with *Coleogyne* and *Yucca*. They were most abundant in association with *Lycium* spp. They were more frequently associated with soil and humus with *Eurotia* and *L. pallidum*, about evenly distributed between the two areas with *Larrea* and *Lycium andersoni*, and more abundant on stems and leaves of other plants.

Beetles
(Coleoptera)
Figs. 5-15, 18, 24, 29, 35, 37, 38, 42, 46

These were common with all species of plants except *Salsola*, being most abundant with *Yucca*.

With *Larrea* they were about evenly distributed between stems-leaves and soil-humus. With *Lycium pallidum* they were predominantly in the soil and humus, and with other plants they predominated on the stems and leaves. Highest populations of larvae occurred in March with *Eurotia* and *Lycium andersoni*, April with *Kochia* and *Larrea*, and May with *Coleogyne* and *Yucca*. Adults were most abundant in August with *Atriplex canescens*, *Coleogyne* and *Kochia*.

ANTS, BEES, WASPS AND RELATIVES
(Hymenoptera)
Figs. 5-15, 20, 24, 37

These insects were associated with all species of plants except *Kochia*. They were most abundant with *Coleogyne* and least abundant with *Salsola*. Those of the family Formicidae were most common on *Atriplex confertifolia*, *Coleogyne*, *Grayia*, *Larrea*, *Lycium pallidum* and *Salsola*, whereas other families were most common with other plants. With *Lycium andersoni* these insects were about evenly distributed between stems-leaves and soil-humus. With *Atriplex canescens*, *Eurotia* and *Larrea* they were more abundant on stems and leaves, whereas with other plants they were predominant in the soil and humus.

FLIES
(Diptera)
Figs. 5-15, 17, 21, 25, 29, 38, 46

These insects were found with all plant species except *Salsola*, and were relatively rare with *Kochia*. They were most abundant with *Yucca*. They were evenly distributed between stems-leaves and soil-humus with *Coleogyne*, *Larrea* and *Lycium andersoni*. They were more predominant in the soil and humus with *Atriplex* spp., and on the stems and leaves of other plants. Highest numbers of larvae occurred most frequently in February with *Atriplex* spp. and *Yucca*, and in April with *Lycium* spp.

DISCUSSION

The collection techniques and procedures in this study undoubtedly biased our results. Approaching a plant and cutting it into small pieces causes many flying insects to leave before they can be collected. Although plants were not disturbed physically before a canvas was set in place, the approach of the collector may have caused some arthropods to drop to the ground. This is known to be a part of the protective behavior of some organisms. All the collections were made during the daylight hours. Thus, the incidence of nocturnal associates and their distribution on the plant or ground is not known. This may explain in part the predominance of stem and leaf dwellers in the soil and humus under the protective cover of the plant. Climatic changes such as wind, precipitation or cloudiness during the day may also influence the movement of some arthropods.

The Berlese funnel likewise was a selective sampling technique. Some arthropods may be heat tolerant or negatively phototaxic and consequently may not have moved down the funnel into the collecting bottle. Others may have been killed by the heat or were unable to pass through the relatively small screen supporting the plant materials.

Nevertheless, on the basis of the techniques used, the results are indicative of incidence, relative abundance and seasonal occurrence of certain groups of arthropods on the plants sampled. These data may serve as a basis for further studies at the test site dealing with the effects of nuclear testing and radiation on food chains, as well as radionuclide pathways.

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ALLRED, D. M., D E. BECK AND C. D. JORGENSEN. 1963a. Biotic Communities of the Nevada Test Site. Brigham Young Univ. Sci. Bull., Biol. Ser., II(2):1-52.

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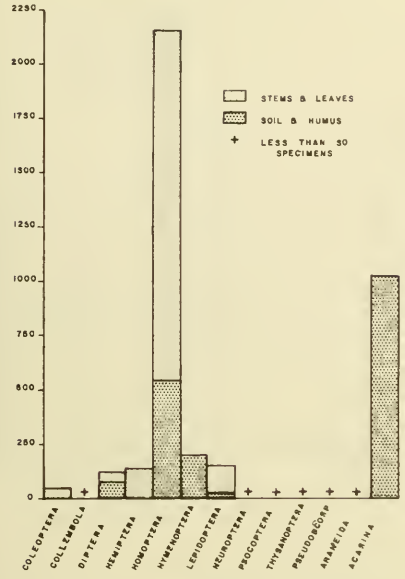

Figure 5. Relative abundance of arthropods associated with *Atriplex canescens*.

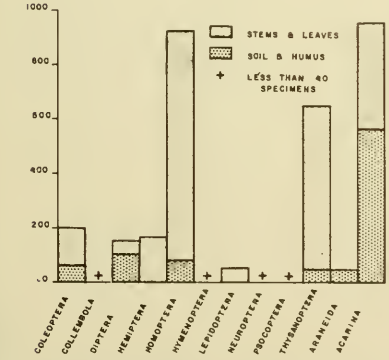

Figure 6. Relative abundance of arthropods associated with *Atriplex confertifolia*.

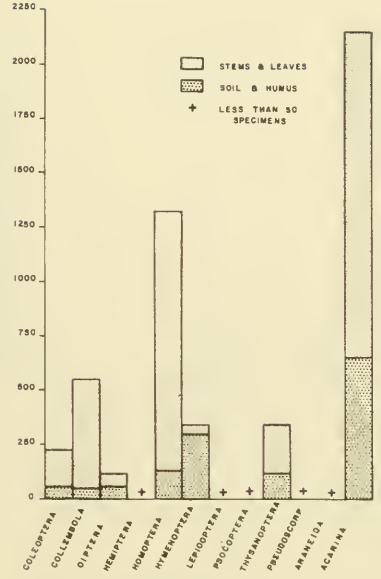

Figure 7. Relative abundance of arthropods associated with *Coleogyne ramosissima*.

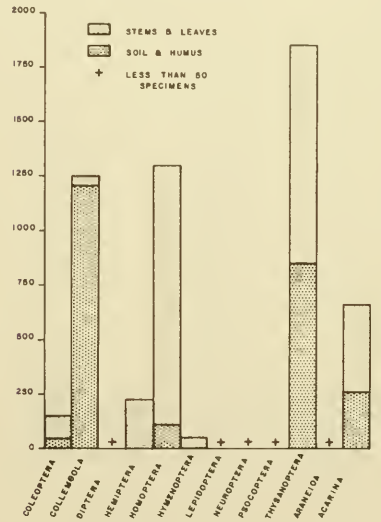

Figure 8. Relative abundance of arthropods associated with *Eurotia lanata*.

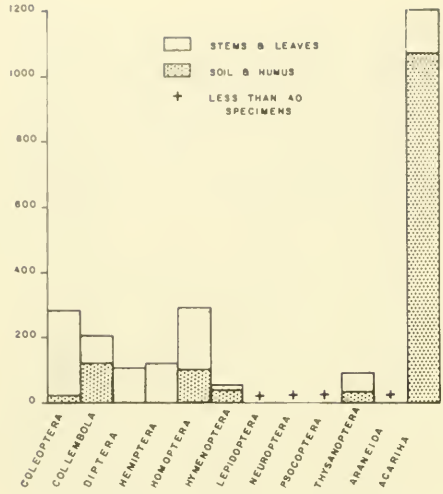

Figure 9. Relative abundance of arthropods associated with *Grayia spinosa*.

Figure 10. Relative abundance of arthropods associated with *Kochia americana*.

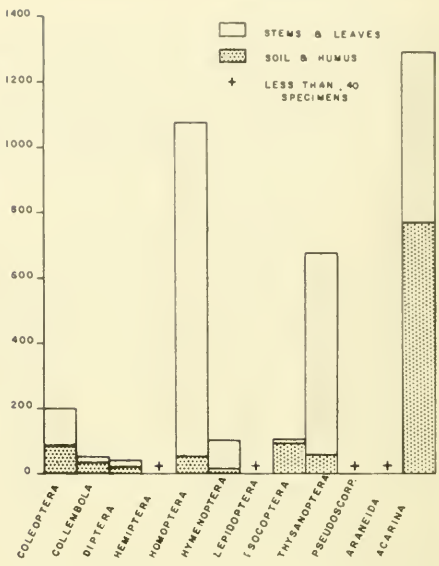

Figure 11. Relative abundance of arthropods associated with *Larrea divaricata*.

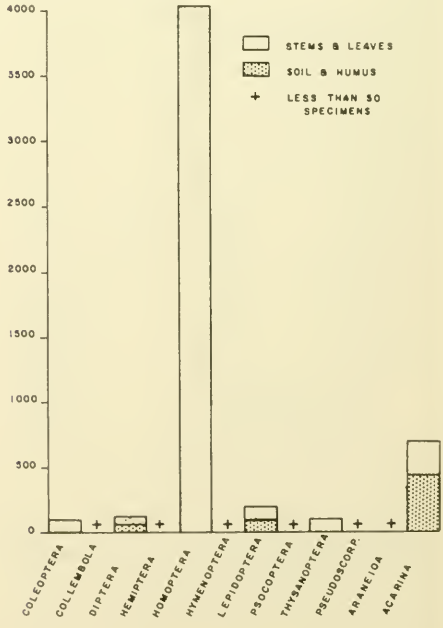

Figure 12. Relative abundance of arthropods associated with *Lycium andersoni*.

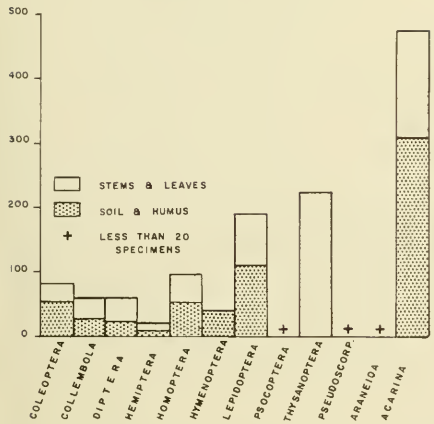

Figure 13. Relative abundance of arthropods associated with *Lycium pallidum*.

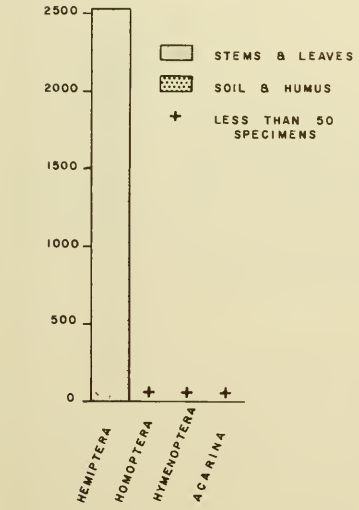

Figure 14. Relative abundance of arthropods associated with *Salsola kali*.

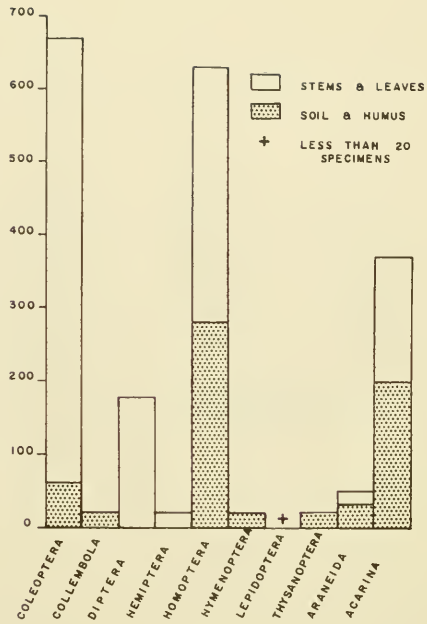

Figure 15. Relative abundance of arthropods associated with *Yucca brevifolia*.

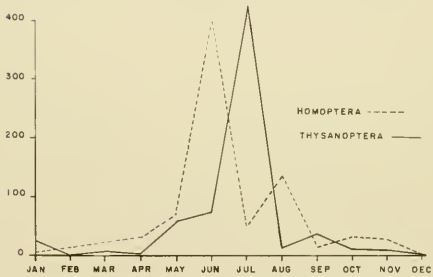

Figure 16. Seasonal occurrence of Homoptera and Thysanoptera on *Atriplex canescens*.

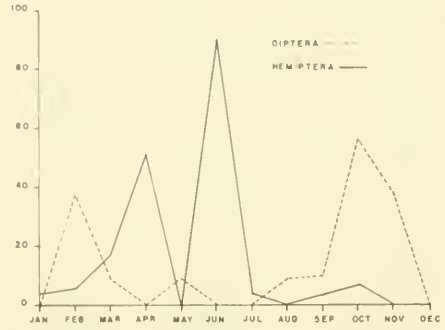

Figure 17. Seasonal occurrence of Diptera and Hemiptera on *Atriplex canescens*.

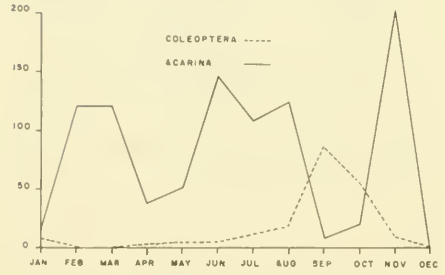

Figure 18. Seasonal occurrence of Coleoptera and Acarina on *Atriplex canescens*.

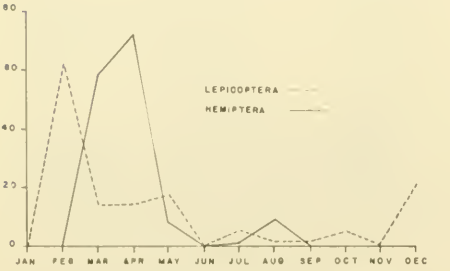

Figure 19. Seasonal occurrence of Lepidoptera and Hemiptera on *Atriplex confertifolia*.

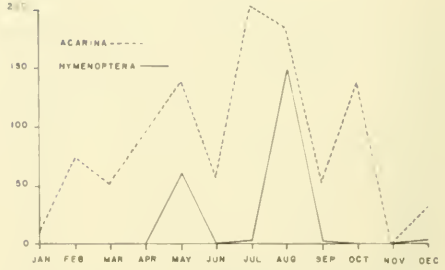

Figure 20. Seasonal occurrence of Acarina and Hymenoptera on *Atriplex confertifolia*.

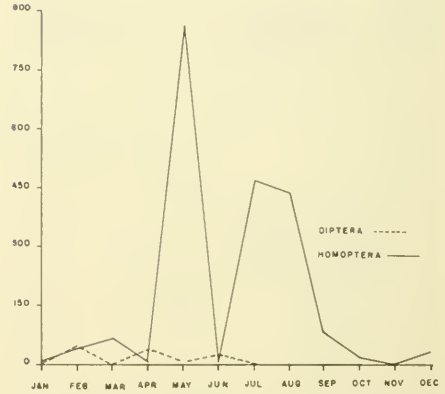

Figure 21. Seasonal occurrence of Diptera and Homoptera on *Atriplex confertifolia*.

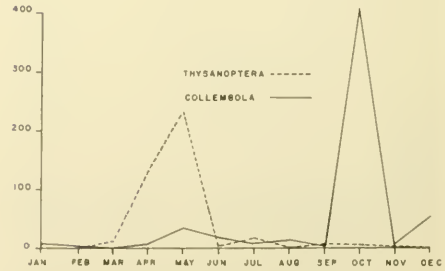

Figure 22. Seasonal occurrence of Thysanoptera and Collembola on *Coleogyne ramosissima*.

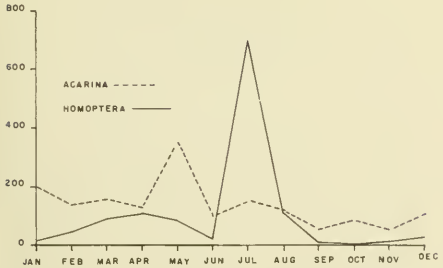

Figure 23. Seasonal occurrence of Acarina and Homoptera on *Coleogyne ramosissima.*

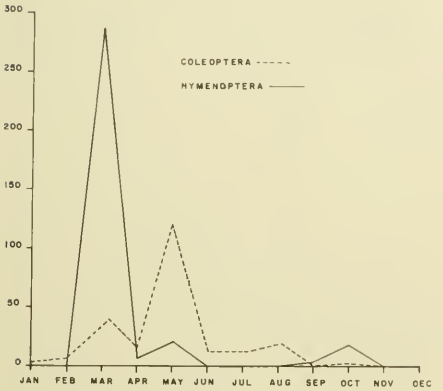

Figure 24. Seasonal occurrence of Coleoptera and Hymenoptera on *Coleogyne ramosissima.*

Figure 25. Seasonal occurrence of Diptera on *Coleogyne ramosissima.*

Figure 26. Seasonal occurrence of Hemiptera on *Eurotia lanata.*

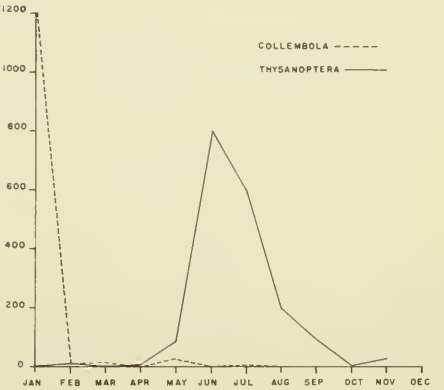

Figure 27. Seasonal occurrence of Collembola and Thysanoptera on *Eurotia lanata.*

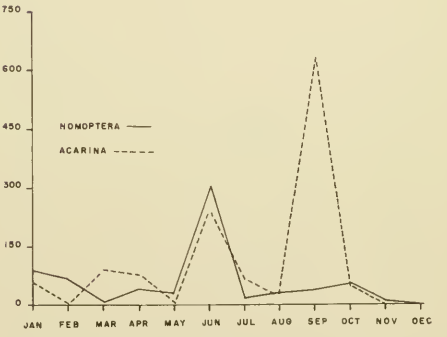

Figure 28. Seasonal occurrence of Homoptera and Acarina on *Eurotia lanata.*

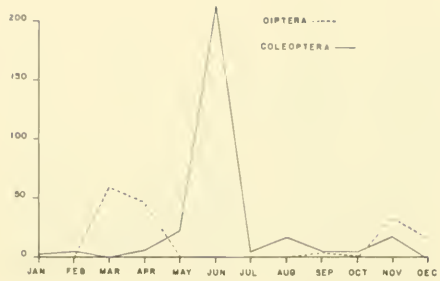

Figure 29. Seasonal occurrence of Diptera and Coleoptera on *Grayia spinosa*.

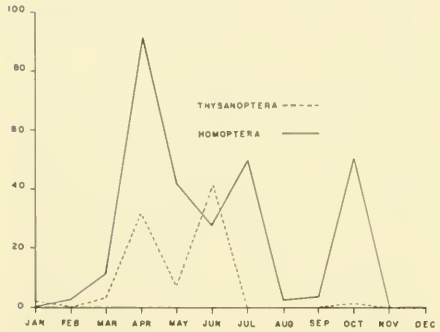

Figure 30. Seasonal occurrence of Thysanoptera and Homoptera on *Grayia spinosa*.

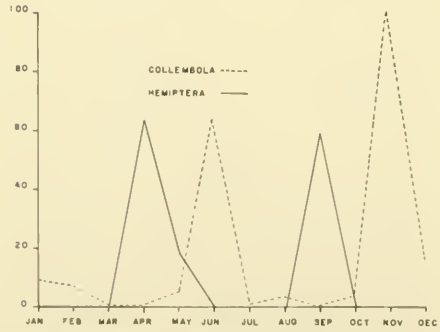

Figure 31. Seasonal occurrence of Collembola and Hemiptera on *Grayia spinosa*.

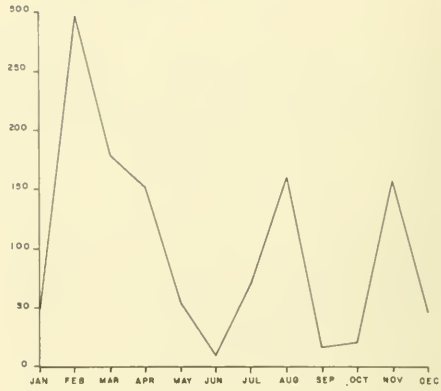

Figure 32. Seasonal occurrence of Acarina on *Grayia spinosa*.

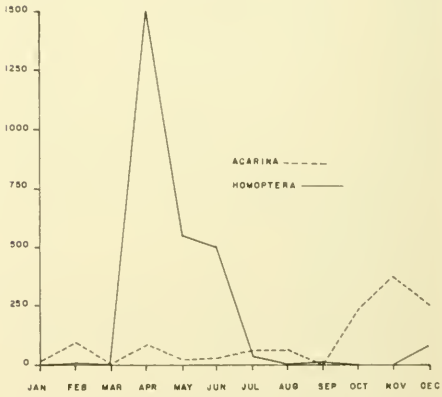

Figure 33. Seasonal occurrence of Acarina and Homoptera on *Kochia americana*.

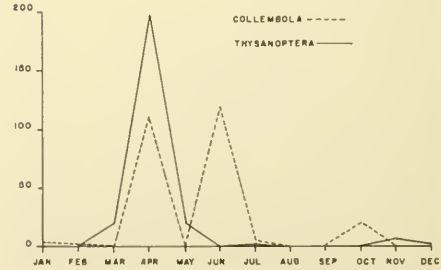

Figure 34. Seasonal occurrence of Collembola and Thysanoptera on *Kochia americana*.

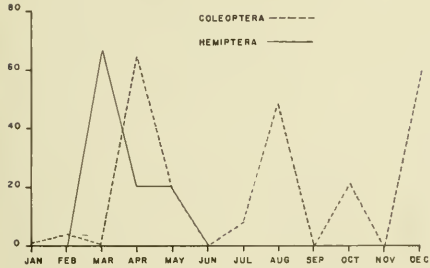

Figure 35. Seasonal occurrence of Coleoptera and Hemiptera on *Kochia americana.*

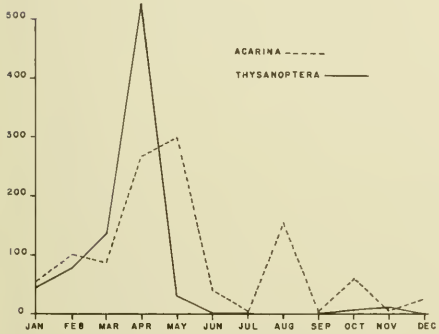

Figure 36. Seasonal occurrence of Acarina and Thysanoptera on *Larrea divaricata.*

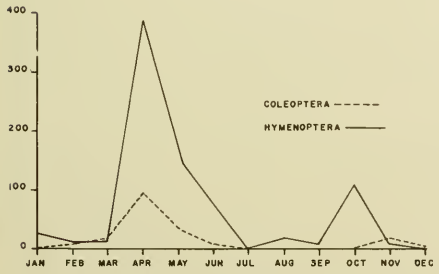

Figure 37. Seasonal occurrence of Coleoptera and Hymenoptera on *Larrea divaricata.*

Figure 38. Seasonal occurrence of Coleoptera and Diptera on *Lycium andersoni.*

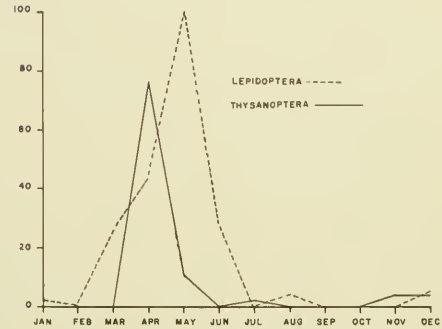

Figure 39. Seasonal occurrence of Lepidoptera and Thysanoptera on *Lycium andersoni.*

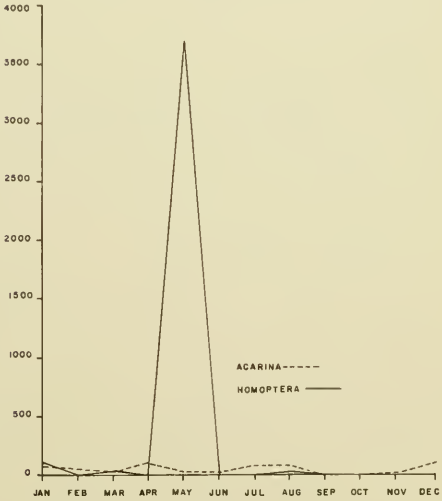

Figure 40. Seasonal occurrence of Acarina and Homoptera on *Lycium andersoni.*

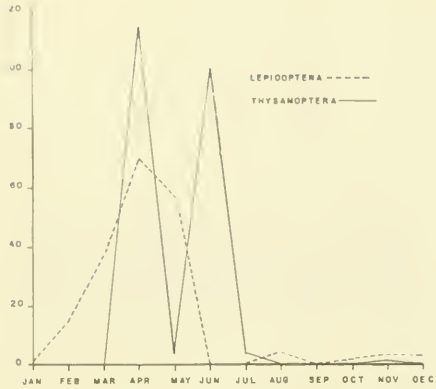

Figure 41. Seasonal occurrence of Lepidoptera and Thysanoptera on *Lycium pallidum*.

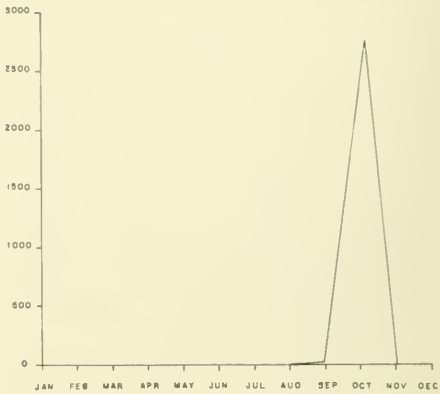

Figure 44. Seasonal occurrence of Hemiptera on *Salsola kali*.

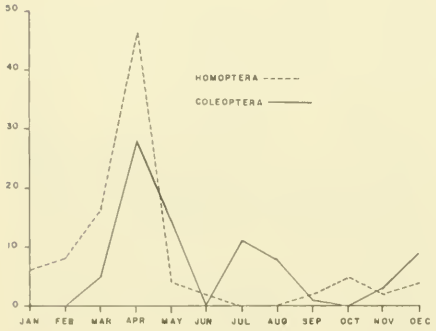

Figure 42. Seasonal occurrence of Homoptera and Coleoptera on *Lycium pallidum*.

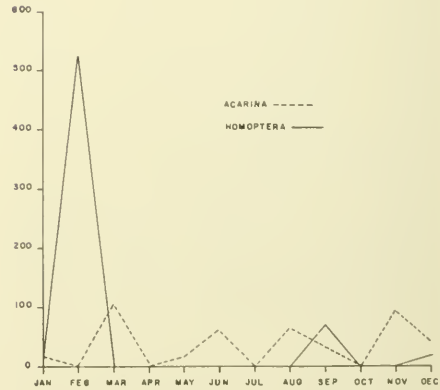

Figure 45. Seasonal occurrence of Acarina and Homoptera on *Yucca brevifolia*.

Figure 43. Seasonal occurrence of Acarina on *Lycium pallidum*.

Figure 46. Seasonal occurrence of Diptera and Coleoptera on *Yucca brevifolia*.

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TABLE OF CONTENTS

	Page
INTRODUCTION	1
MATERIALS AND METHODS	2
OSTEOLOGY	3
Skull	3
Wrist	8
MYOLOGY	11
DISCUSSION	25
Osteology	25
Myology	26
CONCLUSIONS AND SUMMARY	28
LITERATURE CITED	29

LIST OF ILLUSTRATIONS

Fig. 1. Skull of *Sauromalus obesus multiforaminatus*	4
Fig. 2. Skull of *Sauromalus obesus multiforaminatus*	5
Fig. 3. Teeth of *Sauromalus obesus* spp.	7
Fig. 4. Carpal bones from left manus	9
Fig. 5. Carpal bones from left manus	10
Fig. 6. Ventral view of head and thorax musculature, superficial layer and first depth	12
Fig. 7. Ventral view of head and thorax musculature, second and third depths	13
Fig. 8. Ventral view of head and thorax musculature, fourth and fifth depths	14
Fig. 9. Dorsal view of head and thorax musculature, superficial layer and first depth	16
Fig. 10. Dorsal view of head and thorax musculature, second and third depths	17
Fig. 11. Dorsal view of head and thorax musculature, fourth and fifth depths	18
Fig. 12. Lateral view of head and thorax musculature, superficial depth	19
Fig. 13. Lateral view of head and thorax musculature, first depth	20
Fig. 14. Lateral view of head and thorax musculature, second depth	21
Fig. 15. Lateral view of head and thorax musculature, third depth	22
Fig. 16. Lateral view of head and thorax musculature, fourth depth	23
Fig. 17. Lateral view of head and thorax musculature, fifth depth	24
Table 1. Summary of utilized characters	28

Sauromalus obesus obesus
Taken at the Nevada Test Site on rocky hill north of Mercury, June 7, 1960, by Dorald M. Allred. BYU 17435.

INTRODUCTION

The osteological and myological structures of the chuckwallas, genus *Sauromalus*, have long been neglected. Other studies dealing with the taxonomy, physiology, ecology, and general anatomy of *Sauromalus* and of related genera have been made by various workers. Those which are pertinent to this study are cited below. The present study is an attempt to understand the anatomy of the head and neck of *Sauromalus*, to compare it with related genera and to indicate as nearly as possible the phylogenetic position of this genus in the family Iguanidae.

The taxonomy of *Sauromalus* has been reviewed in some detail by Shaw (1945); however, a brief summary of the systematics of the genus, with special reference to the *obesus* group, is pertinent to this paper.

Dumeril (1856) established the genus *Sauromalus* for the species *ater* whose type locality is still unknown. However, Shaw (1945) limits the range of *ater* to those islands off the southeast coast of Baja, California. A series of specimens, collected at Fort Yuma, California, by the Mexican Boundary Survey and Lieut. Ive's Expedition, was described as *Euphryne obesus* by Baird (1858). This genus and species was placed in synonymy under *Sauromalus ater* by Stejneger (1891) and was so considered until 1922 (Schmidt).

Stejneger's paper also distinguished material from Angel de la Guarda Islands, Gulf of California, Mexico, as being different from *Sauromalus ater* Dumeril and the latter being different from *S. ater* of California and Arizona. He reserved judgment on the *ater* problem for lack of specimens, but named the material from Angel de la Guarda Island, *Sauromalus hispidus*.

The Albatross Expedition of 1911 also collected material in Baja and the Islands of the Gulf of California. Dickerson (1919) studied these specimens and from them described three new species. The *interbrachialis* from La Paz proved to be the same as Stejneger's unnamed, doubtful specimen from Espiritu Santo Island. Dickerson also named the species *varius* from San Esteban Island, Gulf of California, and *townsendi* from Tiburon Island, Gulf of California.

Schmidt (1922), who placed *interbrachialis* in synonymy under *ater*, distinguished northern populations of *ater* from southern ones by their greater number of ventral scale rows and resurrected Baird's name *obesus* for the northern population. In the same year Van Denburgh described *S. slevini* from Monserrate Island, Gulf of California, Mexico.

Shaw (1941) studied material from Santa Catalina Island, Gulf of California, Mexico, and described *S. klauberi*. In 1945 he gave full taxonomic treatment to the genus and named *S. australis* from Baja, California and *S. obesus tumidus* from southwestern Arizona. Shaw also concluded that the type locality of *S. ater* must be some island in the Gulf of California rather than the mainland of southwestern United States. This suggestion has helped considerably because the name *ater* had been a source of much confusion to present-day workers. Cliff (1958) described *S. shawi* from San Marcos Island, Gulf of California, Mexico. Recent acquisitions from North Central Arizona and South Central Utah permitted Tanner and Avery (1964) to describe *S. obesus multiforaminatus* from near Hite, Utah.

In a systematic study of the genus *Urosaurus* by Mittleman (1942), a phylogenetic tree for the family Iguanidae was proposed and the primitive position of the genus *Sauromalus* indicated.

Much of the available literature dealing with this genus is concerned with listing and describing of old and new collecting localities. Some such papers are Bocourt (1870-1909), Belding (1887), Mocquard (1899), Van Denburgh and Slevin (1921), Tanner (1927), Bailey (1930), Bogert (1930), Dunn (1931), Cowles (1936), Taylor (1936), Gloyd (1937), Shaw (1946 and 1950), Murray (1955), Gates (1957), W. Tanner (1958), and Smith and Hensley (1959). Distribution patterns in the Great Basin have been discussed by Banta (1961).

Some behavior and physiological studies have also been published. Atsatt (1939) described color changes as controlled by temperature and light. Cowles and Bogert (1944) discussed the thermal requirements of *Sauromalus*, among other genera. Guibe (1954) investigated thermoregulation of reptiles, while Saint-Girons (1956) analyzed the cyclic activities of thermoregulation, and

Cowles (1957) suggested an origin of dermal temperature regulation. Hutchison and Larimer (1960) discussed the reflectability of integuments in the thermoregulation of lizards.

The anatomy of the genus has not been completely neglected as studies concerning the lungs (Salt 1943), blood (Dill and Edwards 1935) and teeth (Hotton, 1955) have been made.

Other studies include food habits both in nature (Shaw 1939) and in captivity (Mayhew 1963), and a paper by Conti and Crowley (1939), describes a new bacterial species from the skin of *Sauromalus varius* Dickerson. Lewis and Wagner (1964) named a new hemogregarine from *Sauromalus* spp. which is vectored by a new mite parasite named by Newell and Ryckman (1964).

Sauromalus and closely related forms have not been overlooked as fossils. *Parasauromalus*, possibly the stem stock for *Sauromalus*, was named by Gilmore (1928) from fragments of a jaw bone and teeth found in sediments of the Middle Eocene, Wind River Formation, of Alkali Creek, Fremont County, Wyoming. These specimens were provisionally referred to as Iguanidae because of resemblances of the dentition to that of *Sauromalus*. Brattstrom (1953-54) reported bits of skin, dentaries, foot bones, skulls, and vertebrae of *Sauromalus* in late Pleistocene deposits in Gypsum Cave, Nevada, where they lay in conjunction with the Ground Sloth, *Nototherium* and the Camel, *Camelops*. Although this material is referred to as being in late Pleistocene deposits, it is more likely of recent age. Gypsum Cave is well within the present range of *Sauromalus o. obesus* and Brattstrom indicates that the fossils closely resemble the modern species.

A basis for morphological study of the Iguanidae has been laid by Davis (1934) and Robison and Tanner (1962), who made a detailed analysis of the osteology and myology of the head and throat regions of *Crotaphytus*, and Oelrich (1956), who studied the head of *Ctenosaura pectinata*.

Some other papers are of importance because they deal with related material. Parker (1880) studied the structure and development of the lizard skull. Cope (1892) was the first to do extensive osteological studies on genera of North American lizards. Studies by Camp (1923), Williston (1925), Goodrich (1930), George (1955), Oelrich (*op. cit.*,) Romer (1956), and Robison and and Tanner (*op. cit.*) have added considerable information to our knowledge of lizard osteology. Statistical studies of the osteology of related genera were made by Phleger (1940) and Lundelius (1957).

Lizard myology began with Mivart (1867) and was followed by the work of Adams (1919), Camp (1923), Romer (1924), Davis (1934), Edgeworth (1935), Olson (1936), Brock (1938), Evans (1939), Kesteven (1944), George (1948), Watson (1954), Oelrich (1956), Sathe (1959), and Robison and Tanner (1962).

The family Iguanidae is unique in its phylogenetic position among modern saurians. This was pointed out by Stokely (1950) in his report on the osteology of the wrist of *Sceloporus*. In his consideration of the wrist elements he discovered an intermedium bone. This wrist element had been considered to be a primitive character and at one time was thought to be restricted to amphibians and extinct reptiles. The possession of this structure by one genus in the family Iguanidae warranted a more detailed study of related forms such as *Sauromalus*. Romer (1956) indicates the presence of an intermedium in unspecialized lizards which he does not identify.

The purpose of this paper is to present an account of the anterior osteology and myology of *Sauromalus* and to investigate its phylogenetic relationships with other Iguanids. All musculature was drawn from an adult specimen of *Sauromalus obesus multiforaminatus*, BYU 29994, and is enlarged approximately one and one half times natural size. Other specimens of *obesus* subsp. were dissected for comparative purposes.

We express our gratitude to those who have aided us in the preparation of this study. We are especially grateful to Dr. J. Keith Rigby for aiding us with the paleontology and to Mr. Ed Kassay and Mr. James Hopkins for their aid in providing us with live specimens to skeletonize and dissect. To those who have been so kind as to read and criticize this study we are grateful and express our thanks.

MATERIALS AND METHODS

Sauromalus obesus obesus Baird and *Sauromalus obesus multiforaminatus* Tanner and Avery are the principal subspecies used in this study. A specimen each of *Dipsosaurus dorsalis* Baird and Girard, *Sceloporus magister uniformis* Phelan and Brattstrom and *Ctenosaurus hemilopha* (Cope) were also dissected for comparative purposes.

Two specimens of *Sauromalus o. multiforaminatus* (BYU 29994 and 21732) from

Crossing of the Fathers, Kane Co., Utah, were examined. Four specimens of *Sauromalus o. obesus* (BYU 21729, 21723, 21728, 21731) came from Calimesa, California. With the exception of BYU 21728 all were males, with snout-vent lengths of 162 mm., 176 mm., 170 mm., and 170 mm., respectively.

A specimen of *Dipsosaurus dorsalis* (BYU 21726) from Calimesa, California, measuring 133 mm. in snout-vent length, was also dissected and compared with *Sauromalus*. An adult *Sceloporus magister uniformis* (BYU 21730) from Washington County, Utah, was also dissected.

All specimens were preserved in formalin. A skeleton of *Sauromalus o. multiforaminatus* and two skulls of *S. o. obesus* were prepared by different methods. The skeleton was prepared by soaking a skinned specimen in 50% ammonium hydroxide for two weeks, with poor results being obtained. A more successful method was to clean the skulls and soak them in Clorox bleach for one hour. Both articulated and disarticulated skulls were studied.

All specimens are accessioned in the natural history collections of Brigham Young University.

The photographs were taken with an X-ray machine using eleven milliamps at one and one half seconds with a medium KVP. By using the X-rays as negatives, the image was enlarged and printed on glossy paper. All work on the intermedium bone was done from these photographs, which proved ample when viewed with a dissecting microscope.

Specimens (all BYU) and species used for the X-ray photographs are as follows: *Sauromalus o. multiforaminatus*, 11734 and 11736; *Sauromalus o. obesus*, 21733; *Dipsosaurus dorsalis*, 21727; *Crotophytus c. baileyi*, 18921; *Crotaphytus w. wislizeni*, 16748; *Holbrookia m. maculata*, 12821; *Callisaurus d. gabbi*, 21270; *Sceloporus m. magister*, 15236; *Uta s. stansburiana*, 14980; *Uta* (*Urosaurus*) *o. ornata*, 192; *Phrynosoma c. frontale*, 15236; and *Ctenosaura hemilopha*, 14618.

OSTEOLOGY

Since an exhaustive study of all skeletal elements is not the primary purpose of this paper, the following discussion will be limited with few exceptions to the skull and wrist bones.

Skull. — In general the skull of *Sauromalus* can be considered to be open with prominent dorsolateral orbital fenestrae dominating the central region of the skull. Posteriorly, in a dorsolateral position, is a large temporal fenestra on each side. Such a structure is a deviation from the typical diapsid condition seen in the fossil ancestors of modern lizards. Ventrally, the orbit floor is also open with an inferior orbital foramen and a pyriform process on each side.

An excellent account and discussion of the skull of *Ctenosaura pectinata* was published by Oelrich (1956:11-39), who described the skull as, ". . . streptostylic, possessing a freely movable quadrate bone which is attached dorsally to the paraoccipital process in two places by a syndesmosis and ventrally to the quadrate process of the pterygoid bone by a diarthrosis . . . kinetic in that the maxillary segment can be elevated and depressed, hingelike, on the occipital segment." Such characteristics can also be demonstrated in fresh specimens of *Sauromalus*, a genus now considered to be closely related to *Ctenosaura*.

Romer (1956:55-217) also gives a rather complete account of the reptilian skull with one section reserved for lizards. In his discussion he figures the dorsal and ventral portions of the skull of *Iguana*.

A fresh chuckwalla skull forms a compact structure which provides for both strength and lightness. The skull is highly complex and the following discussion will serve as a basic description of structures illustrated on Figures 1 and 2. Oelrich (1956) divides his discussion into the occipital and maxillary segments. For convenience such a grouping will here also be followed.

The Occipital Segment forms a median axis for the rest of the skull. It consists of two parts, (a) the Brain Case (basisphenoid, basioccipital, prootic, exoccipital, supraoccipital, and the associated semi-circular canals) and (b) the Foramen Magnum (enclosed by the basioccipital, exoccipitals, and supraoccipital). A tripartate occipital condyle is located on the posterior end of the basioccipital and the lateral exoccipitals.

Basisphenoid (Fig. 1) is the main bone on the floor of the cranium. It is bordered posteriorly by the basioccipital. Dorsally the basisphenoid is attached to the prootic bone and ventrally it articulates with the pterygoids. This bone forms points of origin for the inferior part of the protractor pterygoideus muscle.

Basioccipital (Fig. 1) forms the posterior part of the floor of the brain case and provides areas of attachment for ventral axial musculature. Posteriorly it bears an occipital condyle, and anteriorly joins the basisphenoid and dorsolaterally the exoccipital and prootic bones. This bone provides at-

tachment for the third bundle of the longissimus dorsi muscle.

Prootic forms the anterolateral wall of the brain case and houses part of the membranous labyrinth. At its posterior end the prootic joins the supraoccipital, basisphenoid, basioccipital, and exoccipital. Its anterior borders consist of a series of membranes which form the tunnel for the optic nerve.

The prootic bone provides points of origin for the pseudotemporalis and the protractor pterygoideus muscles.

Exoccipital is formed by the fusion of exoccipital and opisthotic bones. It forms the posterolateral wall of the brain case and the lateral parts of the occipital condyle. Part of the exoccipital houses the posterior portion of the membranous labyrinth. Medialateral articulations form with the parietal, supratemporal, and quadrate bones. At its most lateral projection the exoccipital forms an articulation with the prootic.

The paraoccipital process of this bone serves as an area of insertion for the longissimus dorsi of the axial musculature. The tip of the process receives the insertion of the episternocleidomastoideus muscle.

Supraoccipital forms the roof of the posterior part of the brain case and the dorsal rim of the foramen magnum. It also houses the dorsal part of the membranous labyrinth. Sutures join the supraoccipital to the prootic bone anterolaterally, the exoccipital posteriorly, and the parietal at its anterior extreme.

Orbitesphenoid is a vertical element surrounding the optic foramen. The anterior border forms the posterior margin of the optic foramen and the inferior process forms an area of origin for the superior rectus muscle. The orbitosphenoid also has connections with the prootic bone and the alar process of the basisphenoid.

A combination of bones in the anterior region of the skull is referred to as the Maxillary Segment. It consists of four parts, (a) the Palate (pterygoid, ectopterygoid, vomer, palatine, premaxilla, and maxilla), (b) Orbits (frontal, postfrontal, and jugal), (c) Nasal Capsule (nasal, prefrontal, lacrimal, and septomaxilla), and (d) Temporal Fenestra (parietal, supratemporal, postorbital, squamosal, quadrate, and epipterygoid). These bones are discussed as listed above.

Pterygoid (Figs. 1 and 2) forms the most posterior part of the palate. They are paired bones sutured at the mid-line and comprise the major area of motion between the occipital and maxillary regions. The anterior portion of the pterygoid is sutured to the palatine bone dorsally and the ectoptergoid

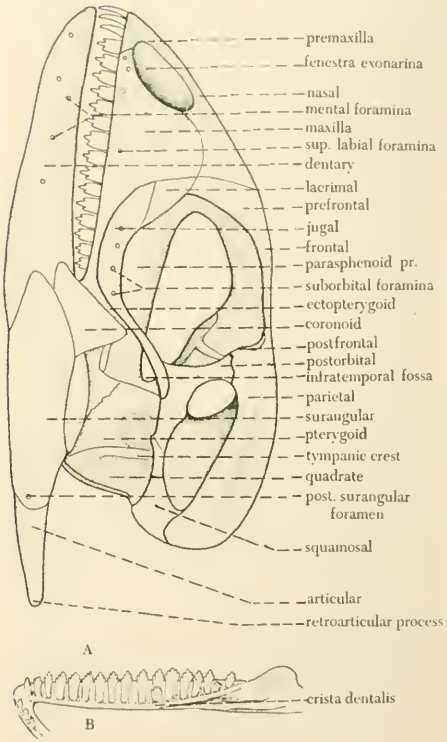

Fig. 1. Skull of *Sauromalus obesus multiforaminatus*, BYU 21734,

A. Lateral view of skull, x 5.

B. Medial view of right mandible, x 2.

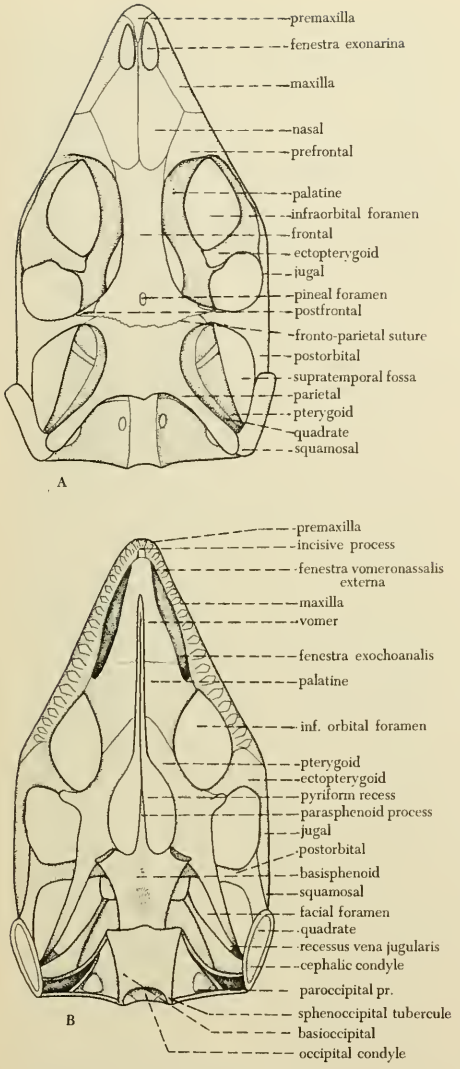

Fig. 2. Skull of *Sauromalus obesus multiforaminatus*, BYU 21734.

A. Dorsal view, x 4.

B. Ventral view, x 4.

bone laterally. A caudolateral portion of the pterygoid articulates with the quadrate bone. At its anterior end there are facets with which the pterygoid articulates with the basipterygoid and columella.

At the ventral border, the pterygoid forms the posterior limit of the oral cavity and contributes an area for origin of the pterygomandibularis muscle. On a dorsal ridge, medial to the columellar fossa, is an area of insertion for the levator pterygoideus muscle. The insertion of most of the protractor pterygoideus muscle is located on the medial surface of the quadrate process of the pterygoid bone. The posterior fibers of the pterygomandibularis muscles arise along the ventrolateral border of the lateral side of the quadrate process.

Ectopterygoid (Figs. 1 and 2, forms a brace between the palate and the external roofing bones, e.g. parietals, etc. It is bordered laterally by the jugal and the posterior process of the maxilla. Mesially the ectopterygoid connects with the pterygoid. Dorsally it forms the posterolateral part of the floor of the orbit.

Vomer (Fig. 2), a pair of bones, forms the most anterior part of the palate, the medial borders of the fenestra vomeronasalis externum and the medial borders of the fenestra exochoanalis. At its posterior end the vomer is attached to the palatines dorsally and the medial surface of the maxilla. At the mid-line the vomers support the nasal septum and the cartilage of Jacobson's organ. At the extreme anterior end the vomer connects with the maxilla.

Palatine (Figs. 1 and 2) forms the main part of the palate, the floor of the orbit and nasal capsule. This bone has three processes: the anterior, or vomerine, forms the posterior floor of the olfactory capsule; the pterygoid process, which attaches dorsally to the pterygoid, forms the medial rim of the inferior orbital fossa and the floor of the orbit; and the maxillary process attaches dorsally to the prefrontal and ventrally to the jugal and maxillary bones.

Premaxilla (Figs. 1 and 2), the most anterior bone of the skull, joins the maxilla laterally and the nasal bones dorsally. It forms the rostrum of the skull.

Maxilla (Figs. 1 and 2) forms the major lateral surface of the snout. The ventral margin bears a single row of pleurodont teeth. There are three protrusions from the main region of the maxilla. The first protrusion is the premaxillary process which overlays, and is attached to, the maxillary process of the premaxilla. Its medial part attaches to the vomer whereas the dorsal extension forms the inferior rim of the fenestra exonarina.

The posterior process of the maxilla is attached to the jugal and lacrimal bones dorsally, and to the ectopterygoid medially. This process forms the lateral part of the rim of the inferior orbital foramen.

The third process of the maxilla extends dorsally to form the lateral wall of the nasal capsule, the posterior rim of the fenestra exonarina anteriorly, and dorsally attaches to the nasal and prefrontal bones.

The maxilla attaches to the palatine bones along the medial border of the palatine shelf.

Nasal (Figs. 1 and 2) forms the sloped top of the snout and partially covers the nasal capsule. The nasals attach posteriorly to the frontals, anteriorly to the premaxillae, and laterally to the prefrontals. Part of the anterior border of the nasal bone forms the dorsal border of the fenestra exonarina.

Prefrontal (Figs. 1 and 2) forms the anterior angle of the orbit. Medially it attaches to the frontal and nasal bones, ventrally to the maxilla and posteriorly to the lacrimal.

Lacrimal (Fig. 1) is a small bone on the anteroventral rim of the orbit. Dorsally it is attached to the prefrontal, anteriorly to the maxilla, ventrally to the jugal, and ventromedially to the prefrontal.

Septomaxilla is found within the nasal capsule where it covers Jacobson's Organ and houses the anterior part of the nasal capsule. Ventrally, it connects with the vomer and maxilla.

Frontal (Figs. 1 and 2) forms the dorsal border of the orbits and the anterior roof of the brain case. At its posterior extreme the frontal is attached to the parietal and postfrontal bones. Anteriorly, it is sutured to the nasal and the prefrontal. The pineal foramen penetrates the posteromedial portions of this bone.

Postfrontal (Figs. 1 and 2) forms a small part of the posterodorsal margin of the orbit. Posteriorly this bone is sutured to the frontal, and laterally to the postorbital and the parietal.

Jugal (Figs. 1 and 2) forms the ventral border of the orbit and a small part of the supratemporal arch. Anteriorly it attaches to the maxilla, ventrally to the lacrimal and palatine bones, and medially to the ectopterygoid. The dorsal surface forms the anteroventral wall of the orbit.

Parietal (Figs. 1 and 2) forms the roof of the posterior part of the skull. It articulates with the frontal and postfrontal anterolaterally and with the postorbital posteriorly and ventrally. Posteriorly the parietal overlays the supratemporal and articulates with the exoccipital and supraoccipital.

The anterior two-thirds of the dorsal surface of the parietal gives origin to the pseudotemporalis superficialis muscle, and the posterior one-third gives origin to the adductor externus medius. The posterior tip of the supratemporal process supplies the origin for a part of the adductor externus profundus muscle. Laterally the parietal bone gives origin to the levator pterygoideus. The posterior border of the parietal provides attachment to the origin of the depressor mandibularis and the insertion of the spinus dorsi, longissimus dorsi, and episternocleidomastoideus muscles.

Supratemporal provides support for the posterolateral angle of the parietal bone. Posteriorly, it articulates with the exoccipital, squamosal, and quadrate.

On the medial border of the anterior part is a partial origin for the adductor mandibularis externus profundus muscle and on the lateral border is the origin of the adductor mandibularis externus medius muscle.

Postorbital (Figs. 1 and 2) forms part of the posterior rim of the orbit. The dorsal part is sutured anteriorly to the postfrontal and posteriorly to the parietal bone. The anteroventral border has connections with the jugal and the posteroventral border to the squamosal.

The ventral free border of the postorbital gives origin to the anterior half of the levator angularis oris muscle whereas the medial surface of the posterior half gives origin to the adductor mandibularis externus superficialis muscle.

Squamosal (Figs. 1 and 2) is attached to the postorbital bone on the posterolateral border of the skull. The expanded posterior part of the squamosal is attached to the dorsal surface of the supratemporal and the quadrate.

The lateral surface of the squamosal provides an area of origin for the adductor mandibularis externus superficialis and part of the levator angularis oris muscle. The medial surface gives origin to the adductor mandibularis externus medius muscle.

Quadrate (Figs. 1 and 2) is found at the posterolateral angle of the skull where it provides the articulating area between skull and lower jaw. It also forms the seat of the middle ear and attachment for the adductor musculature and tympanic membrane.

Mesially the quadrate is attached to the parietal, dorsally to the supratemporal, and laterally to the squamosal bone. Other parts of its dorsal surface provide for the origin of the adductor mandibularis superficialis and adductor mandibularis externus medius muscles. The medial half and its crest serve as origin for the adductor mandibularis posterior muscle. The posterior end of this area attaches to the prootic bone and the quadrate process of the pterygoid.

The tympanic crest serves as a place of attachment for the tympanic membrane and the origin of the adductor mandibularis externus superficialis muscle.

Epipterygoid extends between the parietal and the pterygoid. Its dorsal tip appears to be held in place by the origin of the pseudotemporalis superficialis muscle. The upper one-third of this bone serves as the origin for the pseudotemporalis superficialis muscle. The ventral two-thirds serves the pseudotemporalis profundus muscle as origin.

The lower jaw consists of two paired rami which unite anteriorly in a mental symphysis and each articulates with the quadrate of the skull posteriorly. The dentary of each ramus bears a single row of pleurodont teeth (Fig. 1), whereas the remaining bones (articular, surangular, angular, splenial and coronoid) are edentate.

Dentary (Figs. 1 and 8) is the largest bone of the lower jaw and bears teeth on its dorsomedial border. At its posterior margins the dentary interdigitates with the coronoid, splenial, angular, articular, and surangular. The ventral border provides the origin for the anterior fibers of the mandibulohyoideus I and III and the genioglossus muscles.

Articular (Fig. 1) is that part of the mandible which articulates with the quadrate of the skull. This bone with its retroarticular process serves as the point for insertion for the depressor mandibularis, intermandibularis posterior, fibers of the pterygomandibularis, and adductor mandibularis externus muscles. The medial border is sutured to the splenial bone.

Surangular (Fig. 1) forms the lateral wall of the posterior third of the mandible. The dorsal border serves as the area of insertion for the adductor mandibularis externus muscle, and the intermandibularis posterior muscle inserts on its lateral surface.

Angular (Fig. 8) is a flat bone whose posterior part forms the ventral surface of the jaw between the articular and surangular. The anterior process of the angular attaches to the dentary. Part of this bone serves as the origin for the mandibulohyoideus I muscle.

Splenial is found on the mesial side of the jaw where it connects with the angular, articular, surangular, dentary, and coronoid bones. The intermandibularis anterior profundus muscle has its origin on this bone.

Coronoid (Fig. 1) straddles the other bones of the jaw from a dorsal position. The two anterior extremities articulate with the dentary and surangular laterally, and the dentary, splenial, and articular bones ventrally.

The posterior, lateral, and apical surfaces give rise to the insertion of the adduc-

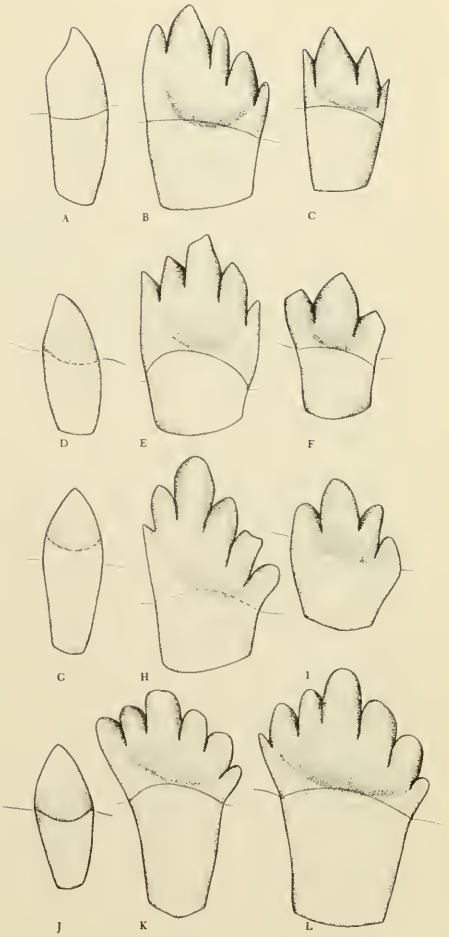

Fig. 3. *Sauromalus obesus multiforaminatus.* BYU 21734. x 11.

A. Most anterior tooth on left side of upper jaw.
B. Eighth tooth from the posterior on left side of upper jaw.
C. Most posterior tooth on left side of upper jaw.
D. Most anterior tooth on left side of lower jaw.
E. Eighth tooth from the posterior on left side of lower jaw.
F. Most posterior tooth on left side of lower jaw.

Sauromalus obesus obesus. BYU 21723. x 11.

G. Most anterior tooth on left side of upper jaw.
H. Eighth tooth from the posterior on left side of upper jaw.
I. Most posterior tooth on left side of upper jaw.
J. Most anterior tooth on left side of lower jaw.
K. Eighth tooth from the posterior on left side of lower jaw.
L. Most posterior tooth on left side of lower jaw.

tor mandibularis externus and adductor medius muscles, and provide an attachment surface for the bodenaponeurosis.

Teeth. — The teeth (Fig. 3) are pleurodont and are borne by the dentary in the lower jaw and the premaxilla and maxilla of the upper jaw. The average number of teeth for each upper jaw is nineteen with the same number occurring in each dentary.

A tooth of *Sauromalus obesus multiforaminatus* may have a variable number of from three to six cusps. Those with six cusps appear to occur only in the anterolateral series with the most posterior teeth having the sixth cusp reduced or missing. In the most anterior teeth one to three cusps appear to be typical. The general pattern on all teeth appears to be a primary cusp with one to three accessary cusps on each side. The crowns are spatulate and about twice as wide as the root.

Gilmore (1928:27-28) described a fossil from the Middle Eocene, Wind River Formation of Fremont County, Wyoming. This specimen, *Parasauromalus olseni*, consisted of two dentaries with fourteen teeth still intact. According to Gilmore, "The teeth present a style of crown structure not before observed among fossil sauria, its closest resemblances being with the living *Sauromalus ater*. . . . The teeth are pleurodont, . . . crowns laterally compressed, acutely spoon shaped, with tip directed inward as in *Sauromalus*." He also indicated that his type specimen represented an individual slightly larger than an adult *Sauromalus ater*.

Hotton (1953:96-97, 105, 107, 111-112) also gives a detailed description of *Sauromalus* dentition and compares it with several other Iguanid lizards. He concludes that "Dentition of *Dipsosaurus d. dorsalis*, *Sauromalus obesus*, and *Ctenosaura similis* are similar to each other and as a group are highly distinctive. Diets are also similar and highly distinctive."

WRIST. — An outstanding feature of the lizard wrist is the presence or absence of the intermedium bone. This bone has been regarded as highly characteristic of lower tetrapods, particularly the amphibians, extinct reptiles and turtles. As the above list suggests, possession of such a bone is an indication of primitiveness.

Until recently the possession of an intermedium bone by some lizards was not suspected. Its occurrence has been reported for families of the old world, primarily Agamidae and the cosmopolitan Scincidae. Camp (1923) indicates that the intermedium is always small and frequently absent in lizards, but does not specify the groups involved. Williston (1925) did not find the bone in the Sauria he examined. Barrows and Smith (1947) found the bone to be present in *Xenosaurus grandis* (Xenosauridae). Stokely (1950:180-181) states, "I found no intermedium in the following species: *Coleonyx variegatus* (Gekkonidae); *Agama caucasica* (Agamidae); *Polychrus marmorata*, *Uma notata*, *Crotaphytus wislizenii* (Iguanidae). In a specimen of *Sceloporus magister*, an x-ray picture shows what I believe to be an intermedium, but I cannot identify it with certainty. . . . However, an intermedium was detected in specimens of each of the following species of the division Autarchoglossa: *Cnemidophorus gularis*, *C. hyperythrus beldingi*, *C. t. tessallatus* (Teiidae); *Xantusia henshawi* (Xantusiidae); *Lacerta erhardi rivoli*, *L. pityusensis grossae*, *L. sicula campestris* (Lacertidae)." Romer (1956:382-383) has an excellent chapter on the carpals of reptiles and states, "The less specialized lizards have a carpal structure which is relatively primitive and readily derived from that seen in *Sphenodon*, but two modifications may be noted: (1) there remains but a single centrale, centrally placed: (2) the intermedium is greatly reduced in size (and readily overlooked) and may disappear completely." However, he does not specify to which groups the above descriptions apply.

The primitiveness of the intermedium bone is not in question. However, the extent of its occurrence in the family Iguanidae is not completely known. One may logically assume that members of the family Iguanidae (other than *Sceloporus*) should possess an intermedium. Phylogenetically the Iguanids are considered to be the stem group from which other lizard groups (Agamids for example) have evolved. Our investigations, including species belonging to ten genera of Iguanids, have confirmed the presence of the intermedium in other genera of this family.

The use of radiographs, in the search for such a delicate structure, has saved time by eliminating the making of serial sections or minute dissections. The resulting photographs show not only small bones, but also indicate a shadow where cartilaginous structures may occur.

The wrist in *Sauromalus* and most other Iguanids seen by us consists of from nine to eleven carpal bones which articulate between the metacarpals and the radius and ulna of the lower arm.

Carpals 1-5 (Figs. 4 and 5) are irregular-shaped bones which articulate at the proximal ends of the metacarpals thus forming the distal row of wrist elements. There are usually five, but one or more may be absent in some specimens. In an adult *Sauromalus* (Fig. 4) all five bones are present, where-

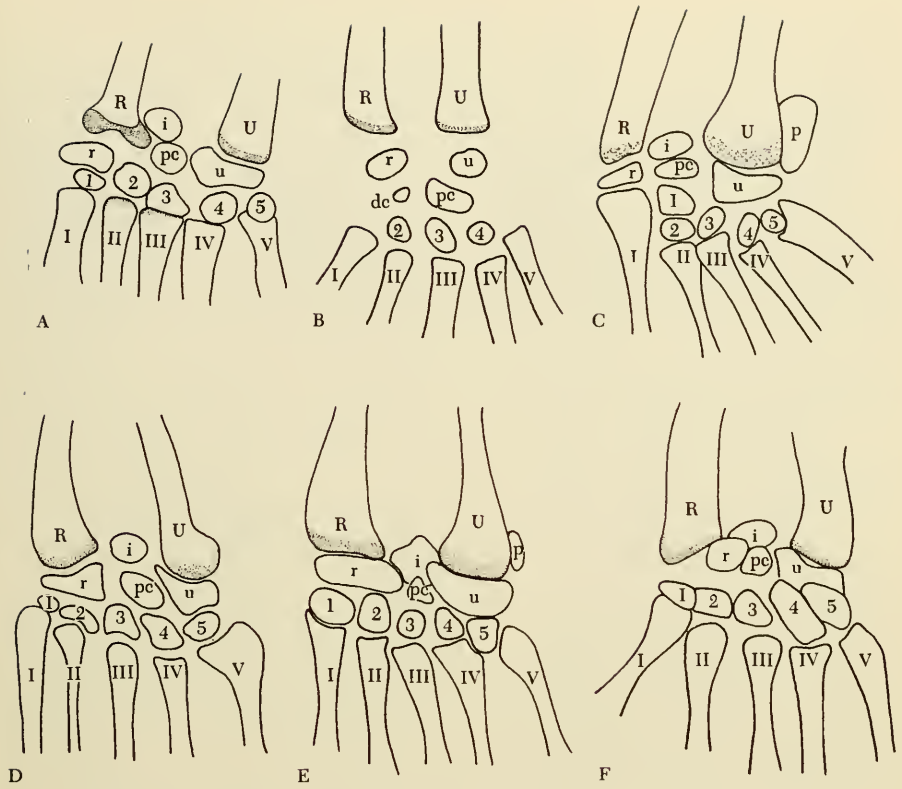

Fig. 4. Ventral view of carpal bones from left manus.

A. *Sauromalus obesus multiforaminatus*. BYU 11736. x 4.
B. *Sauromalus obesus multiforaminatus*. BYU 11734. x 5.
C. *Ctenosaura hemilopha*. BYU 14618. x 5.
D. *Crotaphytus wislizeni wislizeni*. BYU 16748. x 6.
E. *Sceloporus magister magister*. BYU 15236. x 6.
F. *Dipsosaurus dorsalis*. BYU 21727. x 6.

Key to abbreviations used on Figs. 4 and 5: dc-distal centrale, i-intermedium, p-pisiform, pc-proximal centrale, R-radius, r-radiale, U-ulna, u-ulnare, 1-5-carpals, I-V-proximal phalanges.

as in a juvenile (Fig. 4), only four are present.

Radiale (Figs. 4 and 5) is a large carpal found directly distal to the radius. It forms part of the proximal row of carpal elements and was constantly present in all genera examined.

Ulnare (Figs. 4 and 5) articulates at the distal end of the ulna and the proximal end of Carpal 5.

Pisiform (Figs. 4 and 5) is a large carpal shown in the X-ray photographs as being just lateral to the ulna. Several photographs did not show the pisiform to be present. In such cases it may have been obscured by the ulna.

Proximal Centrale (Figs. 4 and 5) appears to be a stable central element in the carpal pattern. It is usually found articulating between Carpals 2 and 3 distally, and the ulnare, radiale, and intermedium proximally.

Distal Centrale (Figs. 4 and 5) can be told from the proximal centrale by its distal position. It appears to be a rather unstable bone and is not present in most specimens as is the case in the adult specimen of *Sauromalus*. It is interesting to note that in the juvenile (Fig. 4) this bone appears to be

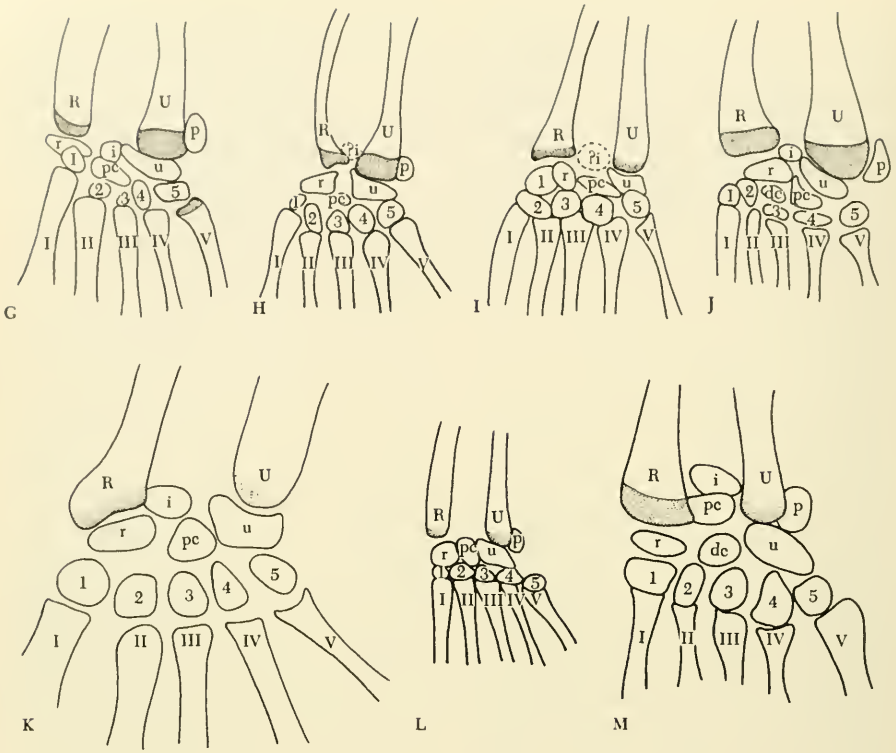

Fig. 5. Ventral view of carpal bones from left manus.

G. *Callisaurus draconoides gabbi.* BYU 21270. x 5.
H. *Urosaurus ornatus ornatus.* BYU 192. x 5.
I. *Uta stansburiana stansburiana.* BYU 14980. x 5.
J. *Phrynosoma coronatum frontale.* BYU 15236. x 5.
K. *Sauromalus obesus obesus.* BYU 21733. x 5.
L. *Holbrookia maculata maculata.* BYU 12821. x 5.
M. *Crotaphytus collaris baileyi.* BYU 18921. x 6.

present. Unfortunately, it may be confused with the distal centrale, which does not appear to be as constant. It is possible that both bones are unstable and that what may be the proximal centrale in one specimen may actually be the distale centrale in another. Romer (1956:380) indicates, ". . . loss of elements from the primitive reptilian carpal (or tarsal) pattern is commonly assumed to be due to fusion."

As observed in Fig. 4, the distal centrale is found mesial to the proximal centrale, distal to the radiale, and proximal to Carpals 1 and 2.

Intermedium (Figs. 4 and 5) is definitely present in *Sauromalus* as indicated in Fig. 4. It is a shadowy structure appearing between the radius and ulna, and proximal to the proximal centrale. In the juvenile specimen (Fig. 4) the intermedium appears as a very faint dense area in the described position. Its shadowy appearance may indicate an incomplete ossification as would be expected.

MYOLOGY

A search of the literature reveals no previous account of the myology of the genus *Sauromalus*. The following account has been prepared by dissection and by using comparative studies of closely related genera.

Sauromalus, Ctenosaura and Crotaphytus appear to be closely related as indicated by the similarity in their musculature and those parts of the skeleton examined. Other studies now in progress which are concerned with other genera of Iguanidae such as *Sceloporus, Uta* and *Phrynosoma* should provide additional evidence of Iguanid phylogeny. Differences in habits and habitat are shown by minor variations of the basic myological pattern. The reader's attention is drawn, in the text, to those differences considered to be comparatively significant. These are discussed in some detail below, but those myological patterns similar to *Crotaphytus*, as reported by Robison and Tanner (1962), and to *Ctenosaura* (Oelrich 1956), are not discussed further.

Specimens used for this study came from Glen Canyon, near Page, Arizona, and Crossing of the Fathers in Southern Utah. They are classified as *Sauromalus obesus multiforaminatus* Tanner and Avery. Specimens of *Sauromalus obesus obesus* (Baird), which were dissected and compared, came from Calimesa, California.

The throat integument is loosely attached to the underlying muscles and is not extendable into a dewlap as in many other Iguanids. However, there is a very distinct gular fold present.

The basic myology of *Sauromalus* has been dissected, illustrated, and compared with *Crotaphytus* (Robison and Tanner 1962) and *Ctenosaura* (Oelrich 1956). The following muscles were found to be similar to those in *Crotaphytus* and *Ctenosaura* and are listed below with their corresponding plate numbers. The plates of Robison and Tanner, and Oelrich, which figure the same muscle, are also listed for comparative purposes.

M. intermandibularis anterior superficialis (Fig. 6); Robison and Tanner — Plate 1; Oelrich — Figs. 36 and 37.

M. mandibulohyoideus I (Fig. 6); Robison and Tanner — Plate 1; Oelrich — Fig. 37.

M. mandibulohyoideus II (Fig. 6); Robison and Tanner — Plate 1; Oelrich — Fig. 38.

M. mandibulohyoideus III (Fig. 7); Robison and Tanner — Plate 2; Oelrich — Fig. 38.

M. genioglossus (Figs. 6 and 7); Robison and Tanner — Plate 2; Oelrich — Figs. 38 and 39.

M. hyoglossus (Fig. 7); Robison and Tanner — Plate 2; Oelrich — Figs. 38 and 39.

M. branchiohyoideus (Fig. 7); Robison and Tanner — Plate 2; Oelrich — Fig. 39.

M. sternohyoideus (Figs. 6, 7, and 13); Robison and Tanner — Plates 1, 2, 7, and 8; Oelrich — Fig. 38.

M. constrictor colli (Figs. 6, 9, and 12); Robison and Tanner — Plates 1, 4 and 7; Oelrich — Figs. 30 and 36.

M. pterygomandibularis (Figs. 6 and 8); Robison and Tanner — Plates 1 and 3; Oelrich — Figs. 32, 35, 37, and 39.

M. levator angularis oris (Fig. 12); Robison and Tanner — Plate 7; Oelrich — Fig. 30.

M. adductor mandibularis externus superficialis (Figs. 6, 8, 9, 12, and 13); Robison and Tanner — Plates 1, 3, 4, 7, and 8; Oelrich — Fig. 31.

M. adductor mandibularis externus medius (Figs. 9, 12, 13, and 14); Robison and Tanner — Plates 4, 7, 8, 9; Oelrich — Figs 32 and 40.

M. adductor mandibularis externus profundus (Fig. 15) Robison and Tanner — Plate 10; Oelrich — Figs. 33 and 41.

M. pseudotemporalis superficialis (Fig. 15) Robison and Tanner — Plate 10; Oelrich — Figs. 33 and 40.

M. adductor mandibularis posterior (Fig. 16) Robison and Tanner — Plate 11; Oelrich — Fig. 34.

M. levator pterygoideus (Figs. 16 and 17) Robison and Tanner — Plates 11 and 12; Oelrich — Figs. 34 and 35.

M. protractor pterygoideus (Figs. 16 and 17) Robison and Tanner — Plates 11 and 12; Oelrich — Figs. 35.

M. trapezius (Figs. 9 and 12) Robison and Tanner — Plates 4, 7, 8, and 9.

M. latissimus dorsi (Figs. 9 and 12) Robison and Tanner — Plates 4, 5, 7, 8, 9, and 10.

M. levator scapulae superficialis (Figs. 8, 10, 13, 14, 15, and 16) Robison and Tanner — Plates 4, 5, 8, 9, 10, and 11.

M. levator scapulae profundus (Figs. 8, 10, 11, 12, and 13) Robison and Tanner — Plates 4, 5, 8, 9, 10, and 11.

M. scapulodeltoideus (Figs. 7, 9, 10, and 13) Robison and Tanner — Plates 2, 4, 5, 7, and 8.

M. serratus (Figs. 10, 11, 14, 15, 16, and 17) Robison and Tanner — Plates 5, 6, 9, 10, 11 and 12.

M. pectoralis (Figs. 6, 7, 12, 13, 14, and 15) Robison and Tanner — Plates 1, 2, and 7.

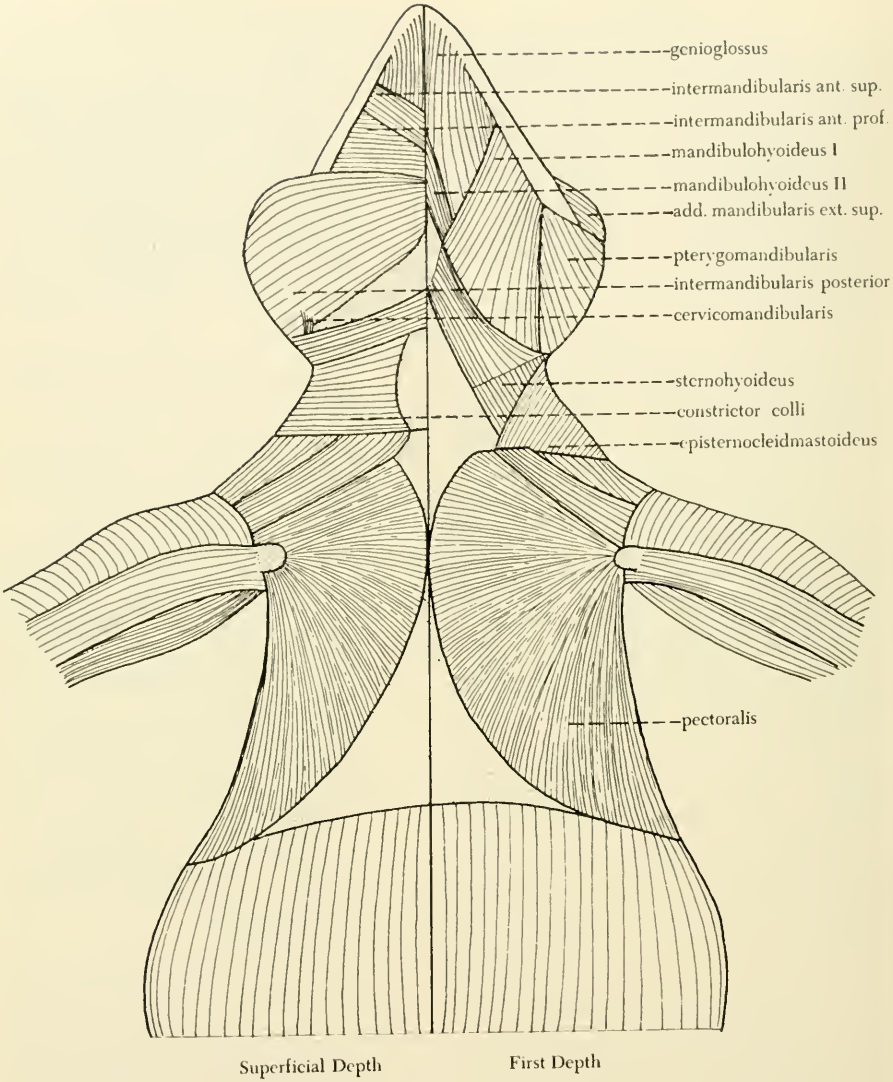

Fig. 6. Ventral view of head and thorax musculature; superficial layer shown at left and first depth at right.

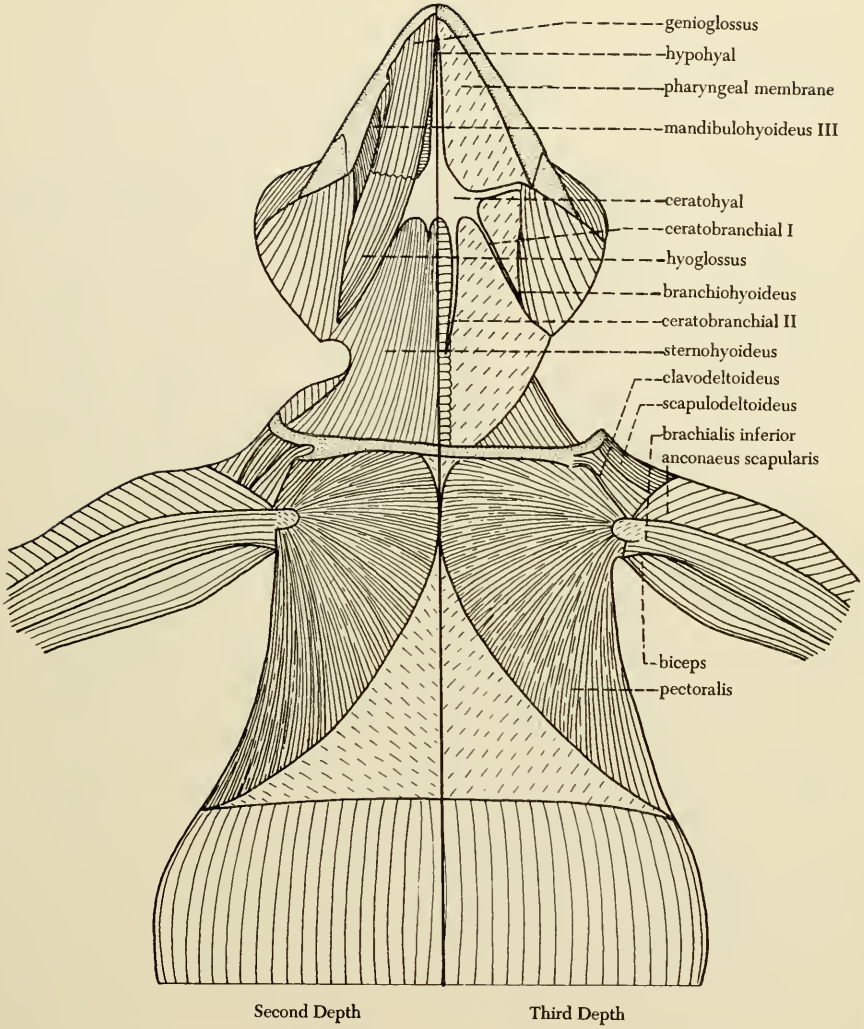

Fig. 7. Ventral view of head and thorax musculature; second depth at left and third depth at right.

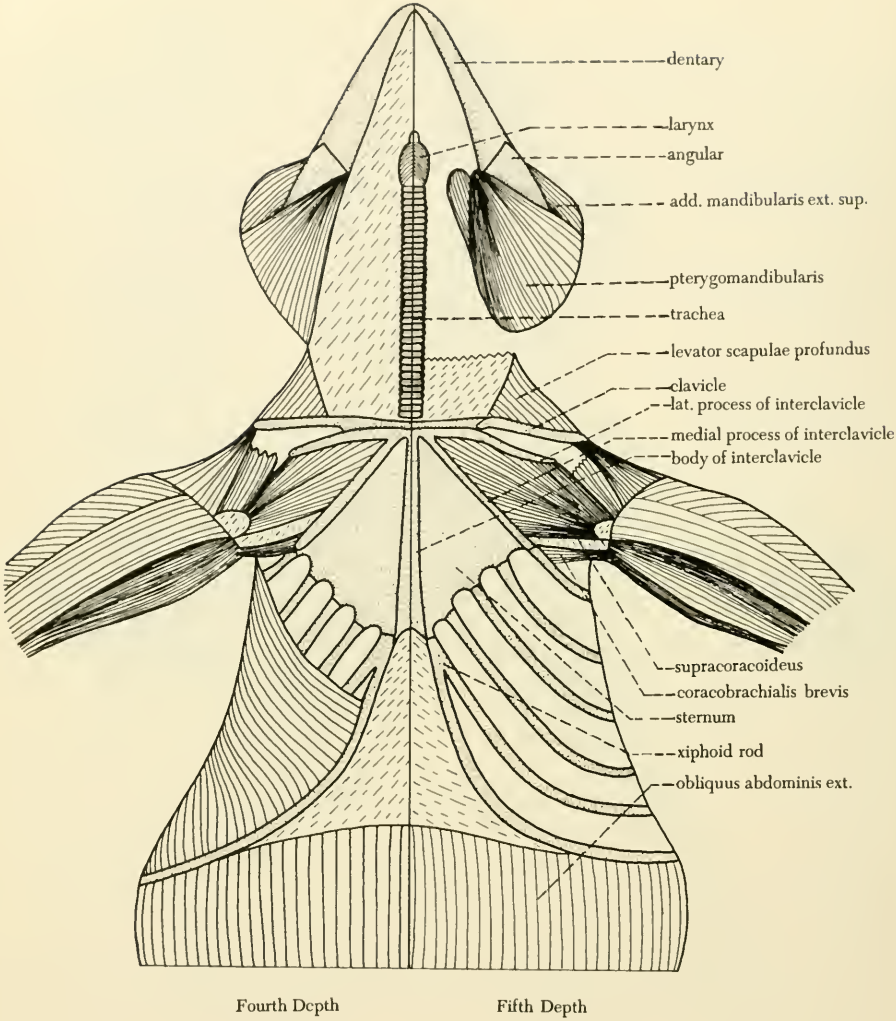

Fig. 8. Ventral view of head and thorax musculature; fourth depth at left and fifth depth at right.

M. clavodeltoideus (Figs. 7, 12, 13 and 14) Robison and Tanner — Plates 2, 7, 8, and 9.

M. supracoracoideus (Figs. 8 and 12) Robison and Tanner — Plates 2, 3, and 7.

M. scapulohumeralis anterior (no illustration) Robison and Tanner — no illustration

M. coracobrachialis brevis (Fig. 8) Robison and Tanner — Plate 3.

M. coracobrachialis longus (Fig. 9) Robison and Tanner — Plates 2 and 4.

M. biceps (Figs. 7, 9, and 13) Robison and Tanner — Plates 2, 4, and 8.

M. brachialis inferior (Figs. 7 and 13) Robison and Tanner — Plates 2 and 8).

M. anconaeus humeralis lateralis (no illustration) Robison and Tanner — Plates 2 and 8.

M. anconacus scapularis (Figs. 7, 9, and 13) Robison and Tanner — Plates 2, 4, and 8.

M. anconaeus coracoideus (Fig. 9) Robison and Tanner — Plate 4.

M. anconaeus humeralis medialis (Fig. 9) Robison and Tanner — Plate 4.

M. subscapularis I (no illustration) Robison and Tanner — no illustration.

M. subscapularis II (Figs. 11, 15, and 16) Robison and Tanner — Plates 6 10, and 11.

M. costocoracoideus (Fig. 16) Robison and Tanner — Plates 11 and 12.

M. internus sternocoracoideus (no illustration) Robison and Tanner — no illustration.

M. externus sternocoracoideus (no illustration) Robison and Tanner — no illustration.

M. sacrolumbalis (Figs. 10, 14, 15, and 16) Robison and Tanner — Plates 5, 9, 10 and 11.

M. obliquus abdominis externus superficialis (Figs. 8, 10, 14, and 16) Robison and Tanner — Plates 3, 5, and 11.

M. obliquus abdominis externus profundus (no illustration) Robison and Tanner — no illustration.

M. intercostales externi (Figs. 11 and 17) Robison and Tanner — Plates 6 and 12.

M. intercostales interni (Fig. 17) Robison and Tanner — Plate 12.

M. obliquus abdominis internus (no illustration) Robison and Tanner — no illustration.

M. transversalis (no illustration) — Robison and Tanner — no illustration.

The following muscles have been found to differ significantly from those of *Crotaphytus* and are discussed in some detail.

M. intermandibularis (Posterior and anterior profundus, Figs. 6, 12, and 13) is a continuous sheet of muscle originating at various points along the lower jaw bones and lies superficial to most of the throat musculature just deep to the skin. The posterior slip of this muscle is extremely thin from its belly to the insertion in the fascia of the midventral area.

The intermandibularis is separable into posterior and anterior parts in *Sauromalus*, with the posterior slip being one muscle fiber thick, with its belly about one-fourth as wide as the belly of the anterior slip. Oelrich (1956:48) also found the intermandibularis to be separable into these two parts in *Ctenosaura pectinata*. We found it to be similar in *Ctenosaura hemilopha*. Robison and Tanner (1962) describe a similar arrangement in *Sceloporus* and *Dipsosaurus*. In the specimens of these genera that we have examined, the posterior slip in *Ctenosaura* is very narrow and cordlike, being only one-tenth the width of the anterior part. In *Dipsosaurus* the division is similar to *Sauromalus*, with the posterior slip being from one-third to one-fourth the width of the anterior. *Sceloporus* shows both bellies widely separated, medially, but with the posterior belly being only about one-sixth the width of the anterior slip.

In *Sauromalus* the two slips are continuous at the origin with the main separation occurring along the mid-ventral line. The anterior slip arises from the mesial surfaces of the splenial and coronoid bones and from the crista dentalis, by a tendon. The anterior fibers extend anteromesially across the throat to insert on the ventral mid-line raphe. The posterior fibers also insert on the mid-line raphe after arising via several interdigitations with the first mandibulohyoideus muscle along the ventral border of the jaw.

The intermandibularis posterior slip of this muscle arises as the last two or three interdigitations of the anterior profundus section with which it is continuous. Posteriorly, this muscle is continuous with the constrictor colli from which it can be delineated by the natural separations of the muscle fiber bundles. The posterior part of the muscle arises from the lateral surface of the mandible with its boundries beginning at the retroarticular process of the articular and passes anteroventrally across the surangular, angular, and the ventral surface of the dentary. Its insertion on the midline raphe is characterized by a wide aponeurosis which leaves both sets of fibers from each side separated. The anteromedial portion of the posterior body in some specimens may be overlain by the insertion of the posterior bundle of the depressor mandibularis.

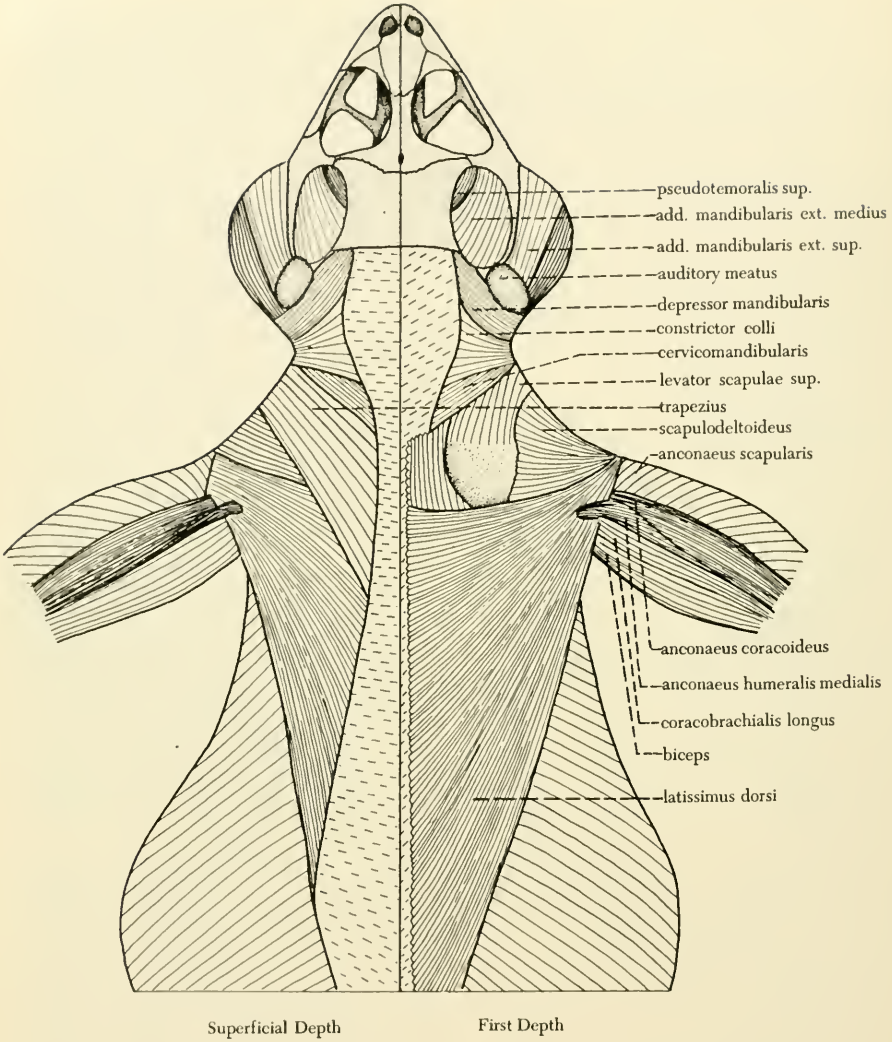

Fig. 9. Dorsal view of head and thorax musculature; superficial depth at left and first depth at right.

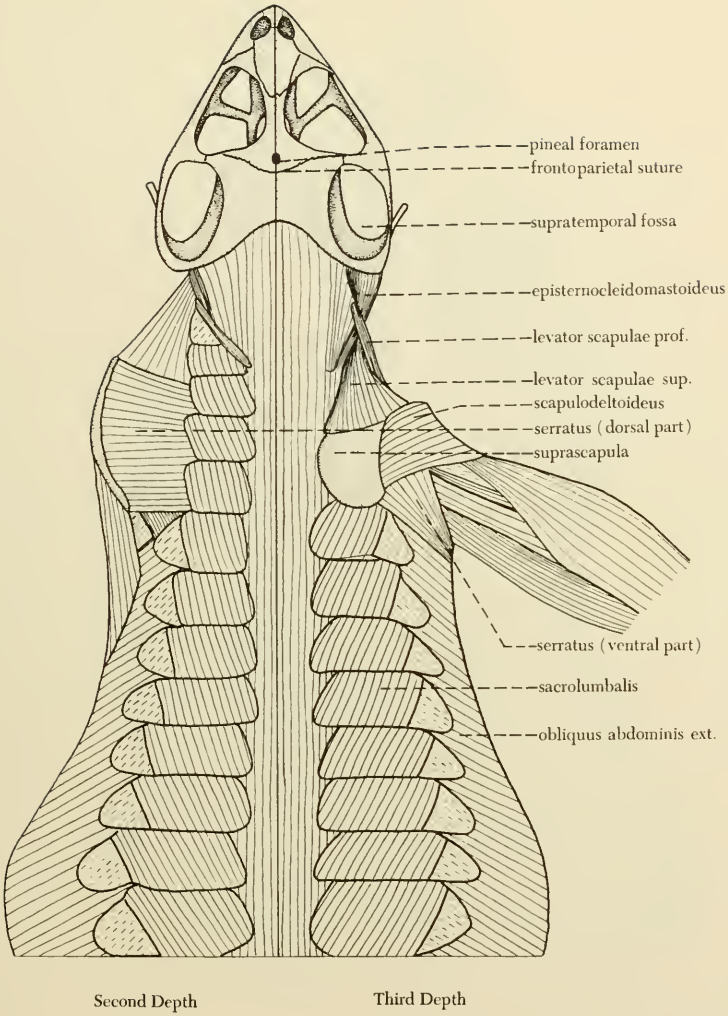

Fig. 10. Dorsal view of head and thorax musculature; second depth at the left and third depth at the right.

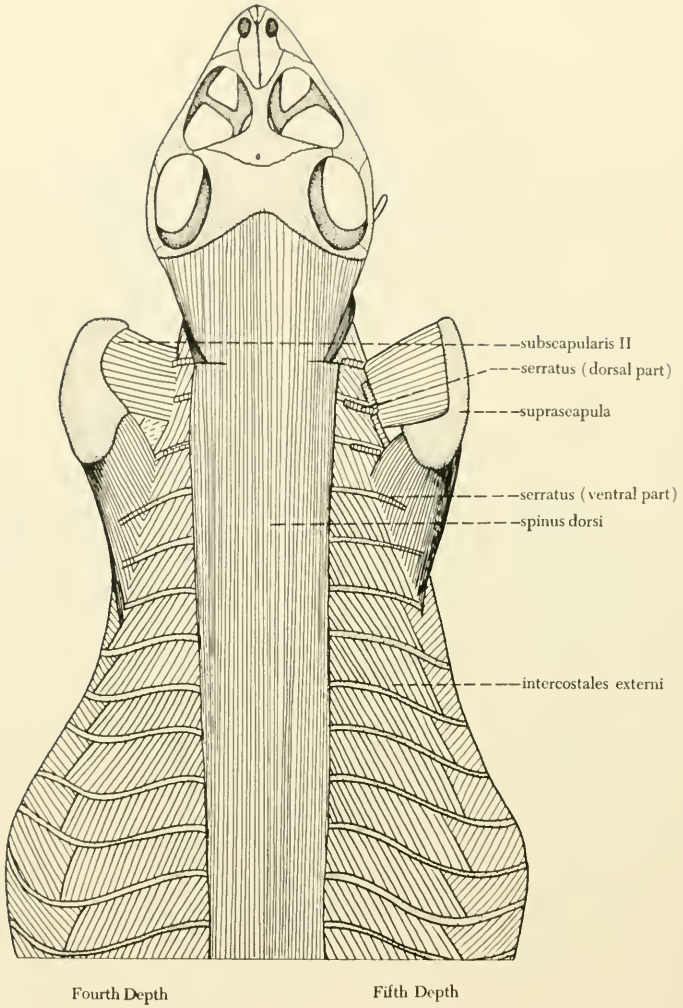

Fig. 11. Dorsal view of head and thorax musculature; fourth depth at left and fifth depth at right.

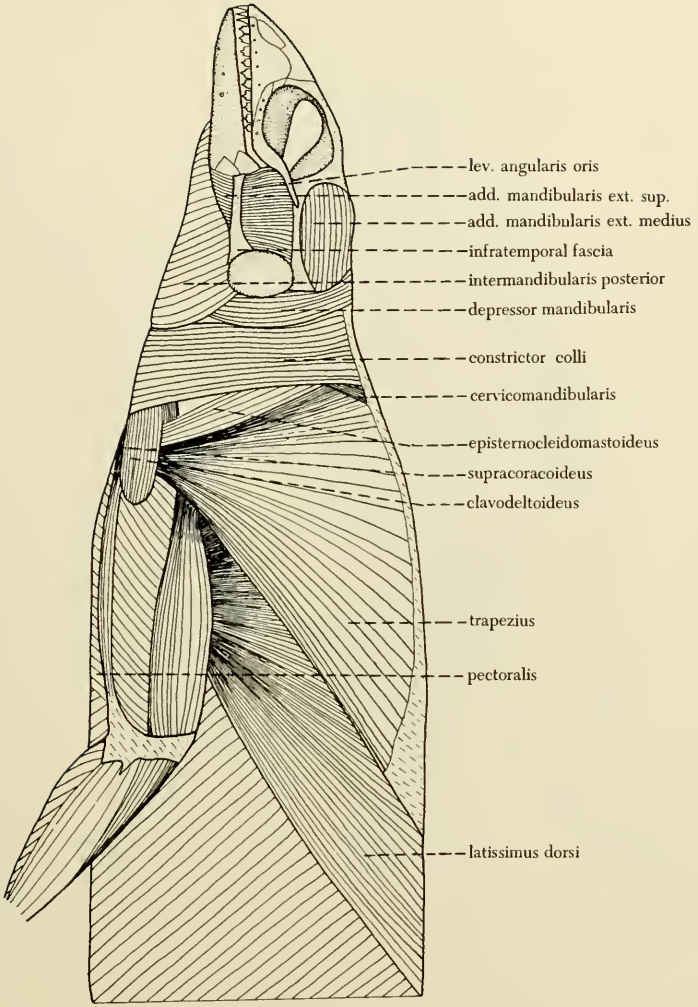

Fig. 12. Lateral view of head and thorax musculature; superficial depth.

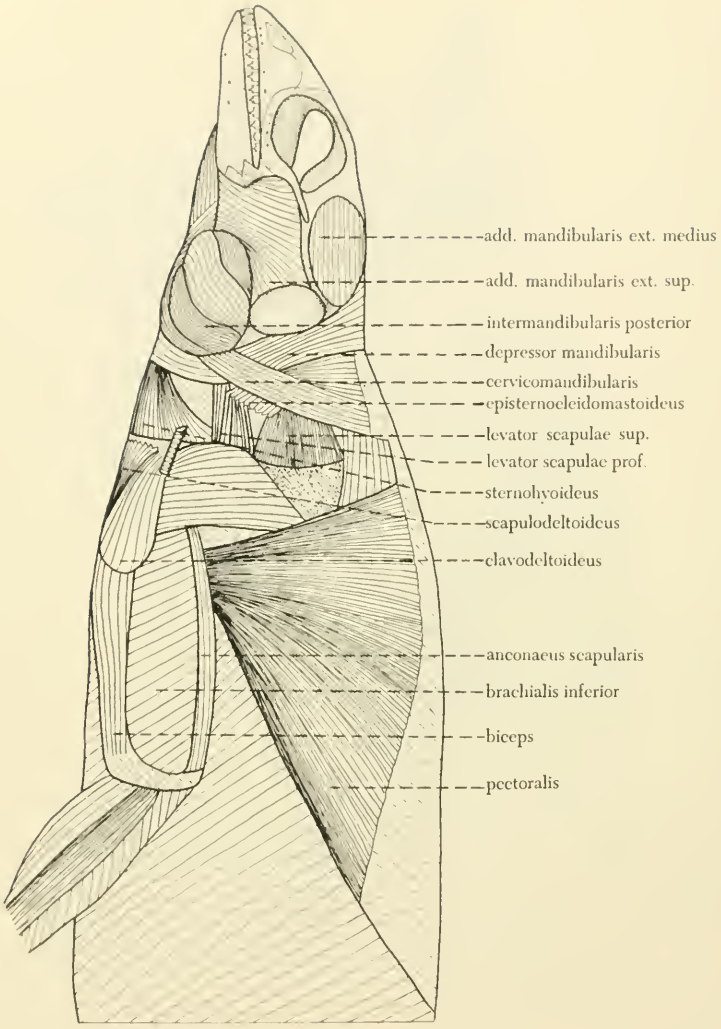

Fig. 13. Lateral view of head and thorax musculature; first depth.

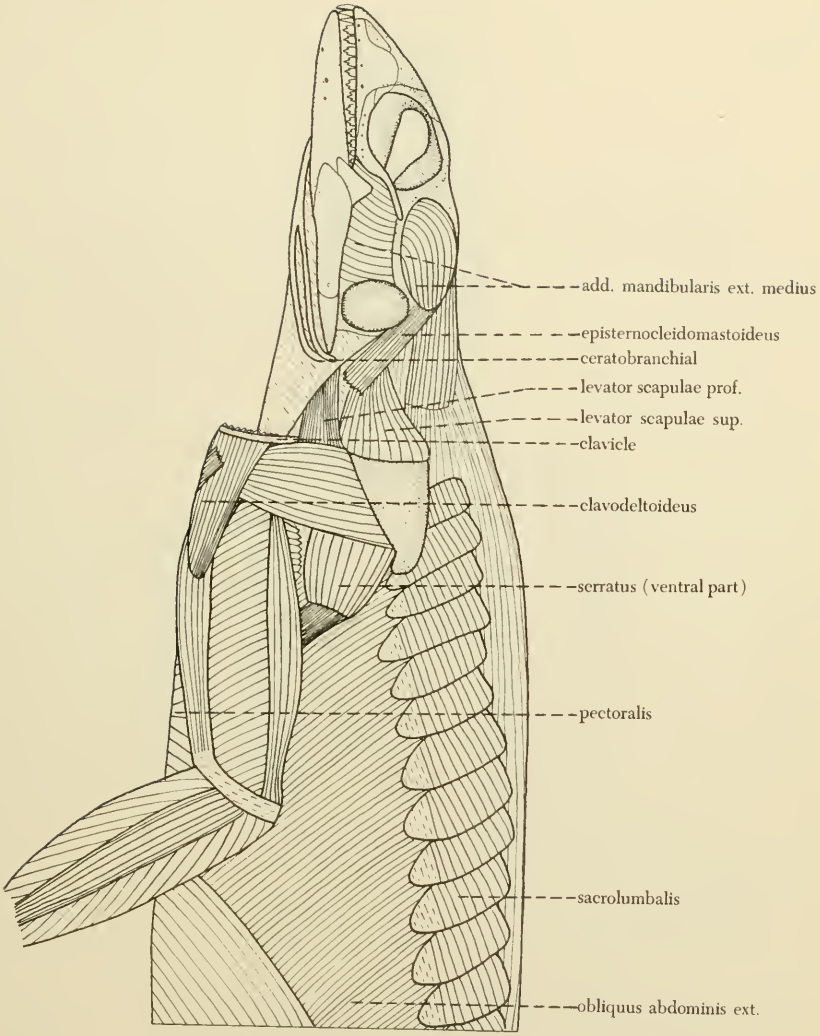

Fig. 14. Lateral view of head and thorax musculature; second depth.

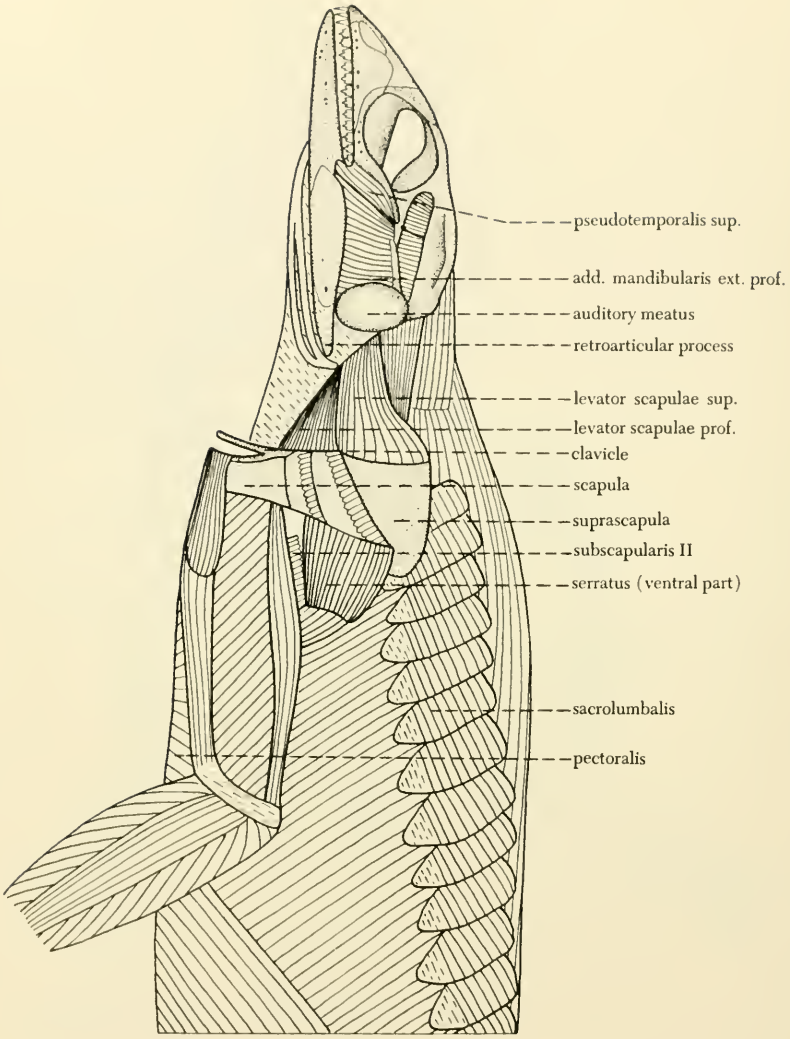

Fig. 15. Lateral view of head and thorax musculature; third depth.

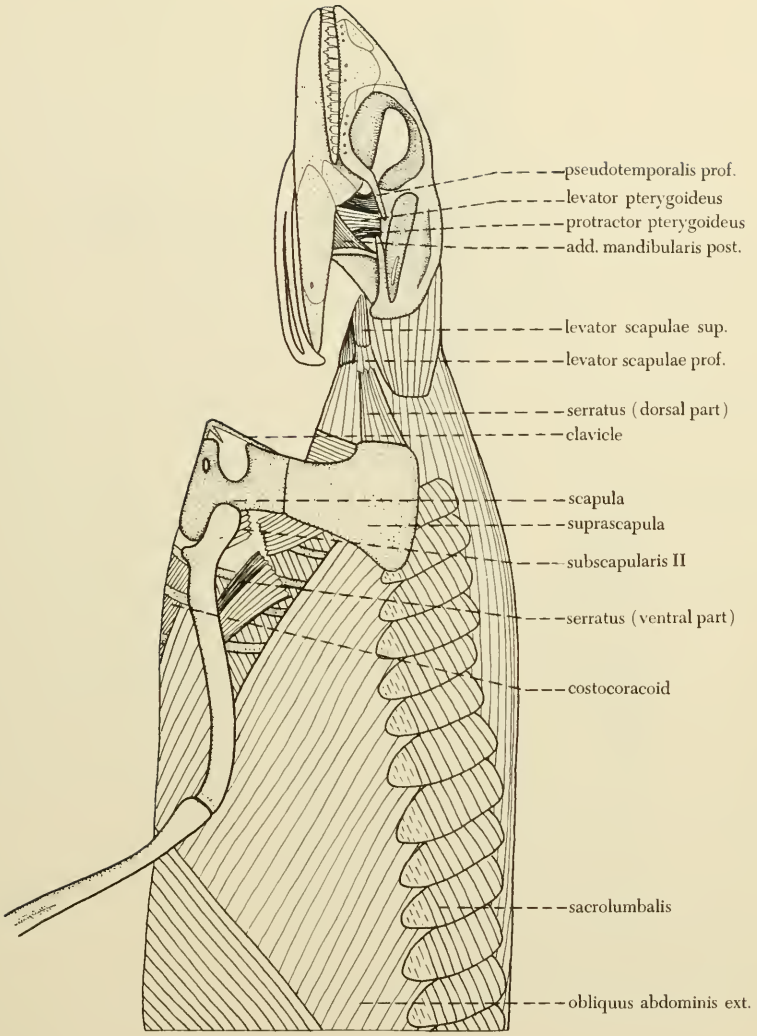

Fig. 16. Lateral view of head and thorax musculature; fourth depth.

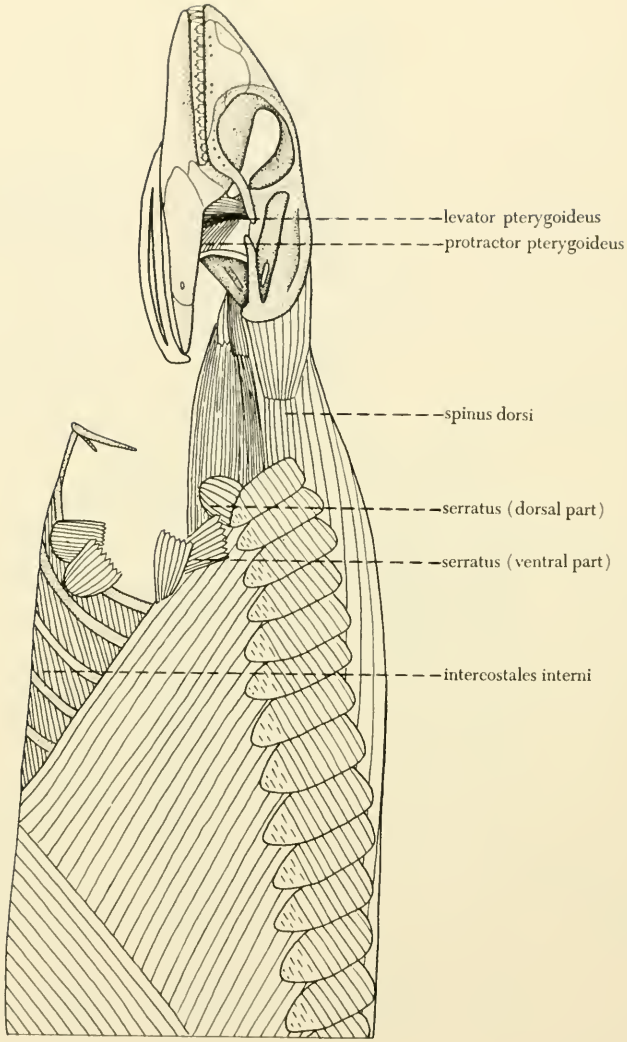

Fig. 17. Lateral view of head and thorax musculature; fifth depth.

M. episternocleidomastoideus (Figs. 6, 10, 12, 13, and 14) is a neck muscle crossing at an oblique angle from the shoulder to the head. This muscle is overlain by the depressor mandibularis which covers its anterior end. Lying deep to the episternocleidomastoideus muscle are the sternohyoideus, the tympanic membrane, the distal ends of the ceratohyal and the ceratobranchial bones, and the two levator scapulae muscles.

The origin appears to be a single head arising from the lateral process of the interclavicle. Robison and Tanner (1962:6-7) have found this to be the case for *Crotaphytus wislizeni*, although there are two heads in *C. collaris* and *C. reticulatus*. Oelrich (1956:48) found a single head in *Ctenosaura pectinata*. We found this condition to also exist in *Sceloporus* and *Diposaurus*.

The insertion occurs on the distal half of the parietal crest, the lateral surface of the paraoccipital process of the exoccipital bone and with some connection to the fascia of the dorsolateral angle of the neck.

M. depressor mandibularis (Figs. 9, 12, and 13) is situated laterally with its anterior edge bordering the auditory meatus posteriorly. It is overlain by the constrictor colli. The anterior part of the depressor mandibularis is superficial to part of the posterior fibers of the adductor mandibularis externus medius and the posterior border of the tympanic membrane. Its posterior parts pass superficially to the anterior fibers of the trapezius and the episternocleidomastoideus, with some lying superficial to the distal ends of the ceratohyal and ceratobranchial bones, and the tympanum.

In *Sauromalus* this muscle is divisible into three bundles as Oelrich (1956:47) indicates for *Ctenosaura* and Robison and Tanner (1962:8) describe for *Crotaphytus wislizeni*.

The origin of the anterior bundle is from the anterolateral surface of the posterolateral parietal wing and parietal crest. This bundle makes up the major part of the depressor mandibularis muscle and passes posteroventrally with a tendinous insertion on the retroarticular process of the articular bone.

The intermediate bundle, in its posterior region, takes origin from the fascia along the dorsolateral angle of the neck, in the region of the first three cervical vertebrae, and ventral to the constrictor colli. This bundle has a common origin with the posterior bundle (cervicomandibularis) and a common insertion, ventrally, with fibers of the anterior bundle, on the retroarticular process.

The posterior bundle is separated by Robison and Tanner (1962:8) under the name cervicomandibularis, and is labeled by that name on Figures 6, 9, 12, and 13 to avoid confusion. Oelrich (1956:47) found it partially connected to the intermediate bundle in *Ctenosaura pectinata*, but described it as ". . . the cervicomandibularis, when separate . . . ." This muscle is completely separate from the other bundles except for a common origin in the superficial fascia of the dorsal mid-line of the neck, which it shares with the intermediate bundle. Its origin is just lateral to that of the intermediate bundle and ventral to the origin of the constrictor colli. It extends anteroventrally along the posterior border of the lateral bundle and continues past the insertion of the anterior and lateral bundles to insert on the superficial fascia of the intermandibularis and the skin.

Robison and Tanner (1962:8) have found the cervicomandibularis to be continuous with the other bundles in old or large specimens of *Crotaphytus*.

The following muscles have not been described previously for the genera involved in this paper, except for a general description of their disposition in *Crotaphytus* by Davis (1934:28).

M. spinus dorsi (Figs. 10, 11, 14, 15, 16, and 17) is a large muscle lying near the midline of the back and occupying the space between the neural spines and zygopophyses of the vertebrae.

This muscle has its origin on the main muscle mass of the caudal region with the main fibers extending anterodorsally to insert on the center of the posterior edge of the parietal bone of the skull.

M. longissimus dorsi is a thick muscle lying lateral to the spinus dorsi and ventral to the sacrolumbalis. At its anterior extremes near the insertion it divides into three major bundles. The most mesial of these emerges from the other two bundles to pass anteriorly and insert on the posterior border of the parietal bone. The second or mesial bundle originates just posterior to the first and passes anteriorly at an oblique angle to insert on the exoccipital. The third or lateral bundle, the most posterior part of the longissimus dorsi, extends anteriorly directly to the basioccipital, where it inserts.

DISCUSSION

Osteology. — The osteological characters of the Iguanid Lizards examined by us appear to be stable, as indicated by a comparison of the skull of *Sauromalus* (Figs. 1 and 2, pp. 3-8) with that of *Ctenosaura* as illustrated by Oelrich (1956), and the general

accounts of reptile osteology described by Williston (1925) and Romer (1956). The bones of the lizard wrist appear to be much less stable than those of the skull. Romer (1956:381) points out that fusion or complete loss of some wrist bones is common in lizards. To quote him, "Loss of elements from the primitive reptilian carpal (or tarsal) pattern is commonly assumed to be due to fusion. Sometimes this is the case, but often assumptions of fusion are unwarranted, and more frequently reductions appear to be due to actual loss of elements."

The most unstable element of the wrist appears to be the distal centrale which is missing in adult *Sauromalus* (Figs. 4, A and 5, K) in *Ctenosaura, Dipsosaurus, Crotaphytus wislizeni, Holbrookia, Callisaurus, Sceloporus, Uta* and *Urosaurus*. This element is present in juvenile *Sauromalus* (Fig. 4, B), *Crotaphytus collaris* and *Phrynosoma*. Romer (1956) indicates that this bone possibly fuses with the proximal centrale. This may explain why the distal centrale is present in juvenile *Sauromalus* and not in the adult. Fusion or deletion may occur later in life.

The intermedium has also been found to be variable in several genera. This wrist element (bone or cartilage) definitely occurs in the following genera: *Sauromalus, Ctenosaura, Dipsosaurus, Crotaphytus, Callisaurus, Sceloporus*, and *Phrynosoma*. It is a questionable structure in *Uta, Urosaurus* and *Holbrookia*. With the methods used in this study, an element as minute as the intermedium would be difficult to locate on small lizards such as the above genera. This may account for the absence of the intermedium in these groups. The possession of such a structure (intermedium) by the above iguanid genera implies that a considerable age or primitiveness may be associated with the family Iguanidae. This structure photographs well in some lizards such as *Sauromalus, Ctenosaura*, and *Crotaphytus* indicating substantial ossification. In *Dipsosaurus, Callisaurus, Sceloporus*, and *Phrynosoma* it appears as a faint shadow on the film, perhaps for lack of ossification. The genera *Uta, Urosaurdus*, and *Holbrookia* appear not to have the structure; however, there is a space for it between the distal ends of the radius and ulna which suggest that if present the intermedium is cartilaginous.

The degree of ossification of this structure and other carpals is probably a function of the age of the individual. This is demonstrated in the genus *Sauromalus* in which the adult (Fig. 4, A) shows the intermedium distinctly, whereas a juvenile of the same subspecies (Fig. 4, B) shows no trace of the bone. There is, however, a space for it between the radius and ulna.

We recognize the need for using larger series in most genera than has been possible in this study particularly when considering elements so small and variable as carpals; however, the data presented seem significant, particularly that dealing with the intermedium and distal centrale.

Teeth. — The teeth (Fig. 3) of *Sauromalus obesus multiforaminatus* and *S. o. obesus* show considerable similarity in their constant size, but differ slightly in shape and position of cusp. The cusps of the teeth of *S. o. multiforaminatus* appear to be more angular than those of *S. o. obesus*. However, this may be due to the age of the specimens, illustrated. The angularity of the teeth on Fig. 3, A-F may indicate those of a young specimen while the more rounded cusps found in G-L represent a specimen more advanced in age. Position of the primary and accessory cusps is variable with no prominent trends recognized.

Age is also exhibited by tooth structure in another way. Old specimens have the accessory cusps completely worn away and the primary cusps reduced to a small swelling in both subspecies.

Myology. — Huntington (1903), Brock (1938), and Smith (1960) indicate that the musculature is an unstable morphological structure for major groupings such as orders and classes. For this reason it may be difficult to interpret homologies in the vertebrate categories above the family level. However, myology at the family level appears to be sufficiently stable to be used as a phylogenetic character. Piatt (1935), working with the North American genera of the family Plethodontidae, and Tanner (1952), working with Mexican and Central American groups of the same family, have indicated that the musculature is consistent enough to define genera. Robison and Tanner (1962) compared the myology of the two subgenera, *Crotaphytus* and *Gambelia*, and found that the myology also remained constant. The lizards of the family Iguanidae, which we have examined, show little myological variation between generic groups. This is indicated by the fact that of the forty-eight muscles dissected in *Sauromalus* and compared (see pp. 11-25) with *Crotaphytus* as described by Robison and Tanner (1962) and *Ctenosaura* by Oelrich (1956), only three show significant variation in configuration, origin, insertion, and size. Because the myology is relatively stable in the Iguanids, it may be used as a tool for interpreting phylogenies between genera. Some muscles, such as the intermandibularis,

episternocleidomastoideus, and depressor mandibularis, differ between *Sauromalus, Dipsosaurus, Ctenosaura, Seeloporus,* and *Crotaphytus,* yet indicate close generic relationships between genera in the family Iguanidae.

M. intermandibularis is separable into anterior and posterior parts, with the posterior being over one-fourth as wide as the anterior. Such a separation is also discernible in *Dipsosaurus* and *Seeloporus.* In *Dipsosaurus* the posterior part is from one-third to one-fourth as wide as the anterior whereas in *Seeloporus* it is only about one-sixth the width of the anterior part. Oelrich (1956: 48) describes a separable condition in *Ctenosaura pectinata* with the posterior slip being figured as extremely small and widely separated from the anterior slip. Robison and Tanner (1962:2-3) described this muscle in *Crotaphytus* as complete, with the two slips being inseparable. In a single additional specimen of *C. collaris baileyi* examined, we found this to be the case. The morphology of this muscle indicates that *Sauromalus, Dipsosaurus, Ctenosaura,* and *Seeloporus* are more closely related to each other than any one is to *Crotaphytus.*

M. episternoeleidomastoideus arises as a single head in *Sauromalus* as reported by Robison and Tanner (1962:6-7) for *Crotaphytus wislizeni.* The above authors found two heads in *C. collaris* and *C. reticulatus.* Oelrich (1956:48) reports a single head in *Ctenosaura pectinata* with a small mesial slip. Those specimens of *Dipsosaurus* and *Seeloporus* examined also show a single head. The condition of a single head in the episternocleidomastoideus muscle suggests that *Sauromalus* and *Dipsosaurus* are intermediate forms between *Ctenosaura* and *Crotaphytus.*

The different configurations of this muscle between species in *Crotaphytus* may indicate that this muscle is variable and not suited for phylogenic comparisons in this genus, or these myological variations may indicate and support the distinction of at least subgeneric rank between the two groups (*collaris* and *wislizeni*) now recognized in *Crotaphytus.*

M. depressor mandibularis has three muscle bundles in *Sauromalus* as described by Oelrich (1956:47) for *Ctenosaura.* Robison and Tanner (1962:8) have found three bundles in *Crotaphytus wislizeni* and two bundles in *C. collaris.* The most posterior bundle, cervicomandibularis, appears to be variable in reptiles and has caused much confusion in the literature. As Robison and Tanner (1962:8) indicate this muscle fuses with the medial bundle in old specimens, creating a definite relationship between these two bundles. As a result the cervicomandibularis is considered to be a part of the depressor mandibularis complex in *Sauromalus.*

This study has shown that *Ctenosaura* and *Sauromalus* share in common with *Dipsosaurus* (1) an intermandibularis muscle distinguishable into anterior and posterior parts, (2) an episternocleidomastoideus muscle which arises by only one head, (3) a depressor mandibularis muscle which has three bundles instead of two as described for some species of *Crotaphytus,* (4) the possession of an intermedium bone in the wrist, and (5) an herbivorous diet.

The sharing of common characteristics by *Sauromalus* and *Ctenosaura* might be related to their similar habitats and diet (herbivorous), with each filling a comparable ecological niche. *Dipsosaurus,* a dune and sandy flats dweller, and *Sauromalus,* a rock dweller, both display these same myological characteristics, indicating that the groups involved are related through common ancestry.

Crotaphytus differs from *Sauromalus* in having (1) an intermandibularis muscle that is not divisible into anterior and posterior parts, (2) an episternocleidomastoideus muscle which arises by more than one head, (3) a depressor mandibularis muscle which has only two bundles in some taxa, and (4) a different diet (omnivorous).

The above differences in musculature indicate that *Sauromalus* is most closely allied to *Ctenosaura* and *Diposaurus,* with which it shares a herbivorous diet and similar osteological characters as previously discussed. *Seeloporus* exhibits all these characters except diet. Mittleman (1942:113) lists *Seeloporus* as a branch from *Ctenosaura,* with *Urosaurus, Utu,* and *Sator* being derivatives of the pre-*Seeloporus* line. Since *Seeloporus* appears to be related to *Ctenosaura* by the similarity in musculature, *Phrynosoma* should have characteristics intermediate between these two genera. Further study is needed to determine if such is the case. Both *Seeloporus* and *Phrynosoma* are known from Pleistocene fossils, as indicated by Gilmore (1928) and Brattstrom (1953).

Mittleman (1942:113) figures *Ctenosaura* as the base stock from which the genera of North American Iguanidae arose. Assuming he is correct, then the placing of *Sauromalus* and *Dipsosaurus,* as early derivatives of this line, is also seemingly plausible, for all three genera show close relationships. The range of *Ctenosaura* in Mexico may indicate that area to be the major region for Iguanid radiation in North America.

The fossil history of *Ctenosaura* is imperfectly known. An Eocene fossil, *Parasauromalus* (Gilmore 1928:27-28), may represent the ancestral stock for *Sauromalus*. Such evidence may indicate that this genus was well advanced toward its present form at this time and had branched away from the pre-*Crotaphytus* line very early. Fossils of *Crotaphytus* do not appear until Pliocene (Gilmore, 1928), with some occurrence in the Pleistocene of California (Brattstrom 1953). To date the fossil record is incomplete and the radiation of *Crotaphytus* from the main Iguanid stock may have occurred at an earlier time. Present knowledge indicates, however, that this genus represents a later branch away from the main stock than that stem which gave rise to *Sauromalus* and presumably *Ctenosaura*.

CONCLUSIONS AND SUMMARY

Those anterior myological characters and the structures of the skull and wrist discussed previously and figured suggest that *Sauromalus*, *Ctenosaura*, and *Dipsosaurus* form a separate and distinct natural grouping. *Iguana* should perhaps be included as well, but was not examined by us.

Sauromalus, *Ctenosaura*, and *Dipsosaurus* share the following characteristics: (1) an intermandibularis muscle divisible into anterior and posterior parts, (2) an episternocleidomastoideus muscle which arises by only one head, (3) a depressor mandibularis muscle divisible into three bundles, (4) an herbivorous diet. The genus *Crotaphytus* differs from the above genera by having (1) an intermandibularis muscle which is not divisible into anterior and posterior slips, (2) an episternocleidomastoideus muscle arising by more than one head, (3) a depressor mandibularis muscle with two bundles in some species, and (4) an omnivorous diet. *Sceloporus*, which has an omnivorous diet in some species and a carnivorous diet in others, shares basically the above indicated similarities with *Sauromalus*, *Ctenosaura*, and *Dipsosaurus*.

An intermedium is present in *Sauromalus*, *Ctenosaura*, *Dipsosaurus*, *Crotaphytus*, *Callisaurus*, *Sceloporus*, and *Phrynosoma*. This structure is of a questionable nature in *Uta*, *Urosaurus*, and *Holbrookia*. The presence of the intermedium in the wrist of the above genera indicates a greater primitiveness in this feature for the family Iguanidae than for those families which lack the structure (Gekkonidae and Zonuridae). This verifies the position and early distinction of *Sauromalus*, *Ctenosaura*, and *Dipsosaurus* as indicated by the many extinct groups of primitive reptiles as well as the family Agamidae (Stokely, 1950), which also possess the structure.

The ranges of the closely related genera *Sauromalus*, *Ctenosaura*, and *Dipsosaurus*, indicate that a radiation of Iguanid lizards took place in Mexico and Southwestern United States during middle Cenozoic time.

Table 1. Summary of Utilized Characters

	Intermedium		Distal Centrale		Intermandibularis		Episternocleidomastoideus		Depressor mandibularis	
	present	absent	present	absent	1 slip	2 slips	1 head	2 heads	fused	separate
Sauromalus — jv.		X	X			X	X			X
— adult	X			X		X	X			X
Ctenosaura	X			X		X	X			X
Dipsosaurus	X			X		X	X			X
Sceloporus	X			X		X	X			X
Crotaphytus collaris	X		X		X			X		
C. wislizeni	X			X	X			X	X	
*Holbrookia**		X		X						
*Callisaurus**	X			X						
*Uta**		X		X						
*Urosaurus**		X		X						
*Phrynosoma**	X		X							

*The musculature of these genera was not investigated.

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IDENTIFICATION OF THE ADULTS, NYMPHS AND LARVAE OF TICKS OF THE *GENUS DERMACENTOR KOCH (IXODIDAE)* IN THE WESTERN UNITED STATES

by

E. P. Brinton, D E. Beck, and D. M. Allred

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TABLE OF CONTENTS

	Page
INTRODUCTION	1
ACKNOWLEDGMENTS	1
REVIEW OF LITERATURE	2
METHODS AND TECHNIQUES	3
RESULTS	8
General Observations	8
Detailed Species Description	8
Dermacentor albipictus	8
Dermacentor andersoni	10
Dermacentor halli	13
Dermacentor hunteri	15
Dermacentor occidentalis	17
Dermacentor parumapertus	19
Dermacentor variabilis	21
DISCUSSION	24
Adults	24
Key to *Dermacentor* males	25
Key to *Dermacentor* females	29
Nymphs	33
Key to *Dermacentor* nymphs	33
Larvae	38
Key to *Dermacentor* larvae	38
CONCLUSIONS	42
REFERENCES	42

LIST OF FIGURES

Figure		Page
1.	Dorsal and ventral views, male *Dermacentor*	4
2.	Dorsal and ventral views, female *Dermacentor*	5
3.	Dorsal and ventral views, nymphal *Dermacentor*	6
4.	Dorsal and ventral views, larval *Dermacentor*	7
5.	Dorsal and ventral views, male *Dermacentor albipictus*	9
6.	Dorsal and ventral views, female *Dermacentor albipictus*	9
7.	Dorsal and ventral views, nymphal *Dermacentor albipictus*	10
8.	Dorsal and ventral views, larval *Dermacentor albipictus*	10
9.	Dorsal and ventral views, male *Dermacentor andersoni*	11
10.	Dorsal and ventral views, female *Dermacentor andersoni*	11
11.	Dorsal and ventral views, nymphal *Dermacentor andersoni*	12
12.	Dorsal and ventral views, larval *Dermacentor andersoni*	12
13.	Dorsal and ventral views, male *Dermacentor halli*	13
14.	Dorsal and ventral views, female *Dermacentor halli*	13
15.	Dorsal and ventral views, nymphal *Dermacentor halli*	14
16.	Dorsal and ventral views, larval *Dermacentor halli*	14
17.	Dorsal and ventral views, male *Dermacentor hunteri*	15
18.	Dorsal and ventral views, female *Dermacentor hunteri*	16
19.	Dorsal and ventral views, nymphal *Dermacentor hunteri*	16
20.	Dorsal and ventral views, larval *Dermacentor hunteri*	17
21.	Dorsal and ventral views, male *Dermacentor occidentalis*	17
22.	Dorsal and ventral views, female *Dermacentor occidentalis*	18
23.	Dorsal and ventral views, nymphal *Dermacentor occidentalis*	18
24.	Dorsal and ventral views, larval *Dermacentor occidentalis*	19
25.	Dorsal and ventral views, male *Dermacentor parumapertus*	19
26.	Dorsal and ventral views, female *Dermacentor parumapertus*	20
27.	Dorsal and ventral views, nymphal *Dermacentor parumapertus*	20
28.	Dorsal and ventral views, larval *Dermacentor parumapertus*	21
29.	Dorsal and ventral views, male *Dermacentor variabilis*	22
30.	Dorsal and ventral views, female *Dermacentor variabilis*	22
31.	Dorsal and ventral views, nymphal *Dermacentor variabilis*	23
32.	Dorsal and ventral views, larval *Dermacentor variabilis*	23

IDENTIFICATION OF THE ADULTS, NYMPHS AND LARVAE OF TICKS OF THE GENUS *Dermacentor* KOCH (IXODIDAE) IN THE WESTERN UNITED STATES[1]

by

E. P. Brinton,[2] D E. Beck [3] and D. M. Allred[3]

INTRODUCTION

In 1910 C. W. Stiles made the following comment as a part of a summary statement to his extensive study of the stigmatal plates of *Dermacentor* ticks: "The specific determination of ticks is attended in many cases with considerable difficulty."

The only difference between the time of Stiles and more than fifty years later is one of degree. Throughout the world today a great deal of attention is being directed to the studies of ticks in the larval, nymphal, or adult stages, due to their implication in disease transmission and the maintenance of reservoirs of infectious agents in nature. Since 1946 the Department of Zoology and Entomology has been conducting ectoparasite natural history surveys in the Great Basin of the western United States. For the last six years tick surveys have been extended to most of the western United States. Through our efforts and the generous cooperation of others a very extensive collection of ticks has been accumulated.

With the reliable keys composed by Cooley (1938), Cooley and Kohls (1945), Gregson (1956) and others, identification of the adult tick collections has been made. Yet even here we have encountered some difficulty in separating such species of adult *Dermacentor* as *andersoni*, *parumapertus*, *variabilis*, and *occidentalis*. The greatest difficulty occurs, however, when nymphal and larval specimens need to be accurately identified.

To facilitate a partial resolution of the problem of identification, we have studied hundreds of ticks from the western part of the United States. This has included the larval, nymphal, and adult stages. Most of the emphasis has been given to external anatomy and morphology. Nevertheless, copious data have been accumulated on geographic and ecological distribution, seasonal occurrence, and host relationships. As a result we have evolved illustrated keys to assist in the specific identification of the several stages of development of ticks belonging to the genus *Dermacentor* in the western United States. Accompanying the keys is a descriptive analysis with illustrations for each of the following species: *Dermacentor albipictus*, *D. andersoni*, *D. halli*, *D. hunteri*, *D. occidentalis*, *D. parumapertus*, and *D. variabilis*.

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Glen M. Kohls and Carleton M. Clifford, United States Public Health Service, Rocky Mountain Laboratory, Hamilton, Montana, have been very helpful in providing loans of specimens, access to data, counsel, advice, and criticism during the course of this study. Eleanor K. Jones of the same laboratory has also been helpful in technical assistance in preparation of specimens.

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zoological unit at Dugway Proving Ground; Clyde M. Senger, Western Washington State College, Bellingham, Washington; Charles L. Douglas, Mesa Verde National Park, Colorado; and Charles Hansen, Desert Game Range, Las Vegas, Nevada. Selby Herrin, graduate student at Brigham Young University, materially assisted in the technical preparation of specimens. All of the tick specimens collected during the B.Y.U.-A.E.C. ecological studies at the Nevada Test Site, Mercury, Nevada, 1959-1964, were available for study. This project was under the direction of D. M. Allred, a junior author of this paper.

Special recognition is given the Institute of Allergy and Infectious Diseases, National Institutes of Health, United States Public Health Service, whose grants in aid (Projects E-1273 and A1-01273-08) in part supported this study. The Department of Zoology and Entomology at Brigham Young University extended assistance in providing space and equipment, plus the rich resource of tick collections made over many years.

REVIEW OF LITERATURE

At the turn of the century there were a number of workers studying ticks in the United States, seriously attempting to devise means of specific identification. Papers by Salmon and Stiles (1901), Banks (1907, 1908, 1910), and the publication by Stiles (1910) concerned with his study of the stigmatal plates of *Dermacentor* species are some of the more important ones which relate to the present investigation. However, Cooley (1938) was the first person to attempt the formulation of keys applicable to western species of hard-bodied ticks. This was initiated in his treatment of the genus *Dermacentor* and *Anocentor* (Otocentor) in 1938. Later, amplification of studies on hard-bodied ticks was made by Cooley in cooperation with Kohls in 1945 and by Cooley in 1946. Gregson (1956) prepared a key to separate adults of three species of *Dermacentor* found in Canada, emphasizing the same characters used by Cooley in 1938. Arthur (1960), in his contribution to the monographic work on ticks begun by Nuttal, *et al.* (1908-1926) essentially represents the work of Cooley (1938) insofar as identification of *Dermacentor* species in the western United States is concerned.

To find reliable anatomical and morphological characters for the determination of species in the immature stages, Russian and American workers have done considerable work with chaetotaxy and general morphology. Moskacheva (1948) worked with the larval and nymphal stages of *Dermacentor marginatus* (Sulz). Lototsky (1948) investigated the general setal arrangement of ixodid ticks. Glashinskaya - Babenko (1949) made a chaetotaxic study of the larvae of the family Ixodidae. Lototsky (1949) made a special study of chaetotaxy for the genus *Dermacentor*. In an independent study of chaetotaxy conducted by Clifford and Anastos (1960), they chose the terminology proposed by Glashinskaya - Babenko (1949), including new names for those setae not heretofore mentioned. Reznik (1950) presented a comparative morphological study of the larvae of the genus *Dermacentor*. Reznik (1956) also completed another general morphological study of the larval stage of *D. marginatus*, including a key to the larval species of *Dermacentor* in Russia. Serdyukova (1955) made a comparative study on the differential characteristics of larvae and nymphs of the ixodid ticks. In studying the larval *Ixodes* occurring in the U.S.S.R., Filippova (1954, 1955, 1958) employed chaetotaxy. Dinnik and Zumpt (1949) presented an anatomical study of the structure of three different types of sensillae as structures which could be used in taxonomic separation. The sensillae they listed were the sensilla sagittiformia (arrow-shaped organs), sensilla haustiformia (spear-shaped organs), and sensilla auriformia (ear-shaped organs). The sensilla sagittiformia were shown to be sensillae and not spiracles as proposed by Salmon and Stiles (1902) and Delpy (1938), and also referred to as such by Oudemans (1906), Zebrowski (1926), and Cooley (1938). Cerny (1957) utilized the presence or absence of a dermal sensilla (sensilla haustiformia) located on the palps to separate the larval stages of *D. marginatus* from *D. pictus* (Herm). Robertson (1961), in his morphological study of the larval stage in the genus *Dermacentor*, emphasized comparative measurements of setal length.

METHODS AND TECHNIQUES

Adult specimens were removed from 70% alcohol and examined in the unmounted condition by the following method. Ticks were supported on a mold of typewriter cleaner putty, permitting manipulation of the specimen to any desired position, with the use of fine-tipped forceps. A pair of A. O. Spencer Universal Illuminators was found adequate for good lighting at a wide range of magnification. A Leitz stereomicroscope was used for magnifications from 10 to 216 diameters.

In making drawings of the adults an ocular grid was used to insure accurate location of anatomical parts. Illustrations were made freehand on Quadrille paper ruled ten squares to the inch. A general penciled outline was made first. With higher magnification, anatomical detail was added.

Nymphs and larvae were studied from microslide mounts. They were prepared by the method described by Brinton and Beck (1963). Live nymphal and larval specimens are best preserved in Oudeman's fluid. This preservative facilitates the extension of the legs. Specimens were removed from the preservative and placed in Nesbitt's clearing solution, where they were allowed to remain at room temperature. An hourly check on clearing was found advisable. Beyond the time when the specimens first appeared to be cleared, an additional period of not more than three hours was allowed. Excessive overclearing is undesirable as this inhibits extension of the legs. It was not always necessary to puncture all engorged specimens, for some readily cleared without puncturing. Best results in mounting the specimens on microslides were obtained by taking them directly from Nesbitt's solution and placing them in a drop of Hoyer's medium previously applied to the slide. Before the cover slip was applied, specimens were oriented in the medium to the desired position. This facilitated later observation under high-power magnification. The mounted specimen was warmed over an alcohol lamp at brief intervals until the legs had been uniformly extended in the warmed medium. The prepared slide was then placed in a warming oven for forty-eight hours at a temperature of about 50°C. This caused further clearing and solidification of the mounting medium. If at the end of twelve to twenty-four hours the legs had contracted from the extended position, rewarming over a flame usually caused them to extend. Mounted slide specimens were ringed with Zut slide-ringing compound. Very little distortion of general body form resulted with this method. Specimens which had been killed and fixed in the Oudeman's preservative cleared much faster than specimens killed otherwise and preserved in 70% ethyl alcohol.

Drawings of the immature stages were made from slide specimens selected from a series. The slides were examined by use of a Zeiss phase-contrast microscope. Selected specimens were placed on a Leitz microslide projector and projected to Quadrille paper ruled ten squares to the inch. A penciled outline was made showing general anatomical features. Anatomical and morphological detail was added to the sketch, after careful examination by use of a phase-contrast microscope. The final drawings were accomplished after comparing the slide-mounted specimens with some which were unmounted. This comparison was made by use of a Leitz stereo-microscope at magnifications of 120-216 diameters. Best illumination of the latter was obtained by the same lighting previously mentioned. In making drawings of slide-mounted specimens, some distortion may be expected. For this reason the final comparative examination with unmounted specimens is very important.

In formulating keys to identify nymphs and larvae, slide-mounted specimens were studied to a considerable extent. It should be emphasized, however, that if adequate lighting and magnification are available, unmounted specimens should be examined. This is especially true for the larvae.

Chaetotaxy has not been utilized for the separation of the species in any of their stages of development. Not only was it felt unnecessary for the separation of the adults and nymphs, but detailed comparisons within a species for these stages showed considerable variation both in position and often in the number of setae. However, in this study idiosomal setae in the larval stage, exclusive of those on the coxal plates, have been labelled for general reference. For a more comprehensive treatment of larval chaetotaxy refer to Clifford and Anastos (1960).

In the formulation of keys, general geographical and altitudinal distribution as well as host relationships have been referred to where necessary to aid in identification of the species.

Figures 1, 2, 3, and 4 are labelled drawings for general reference.

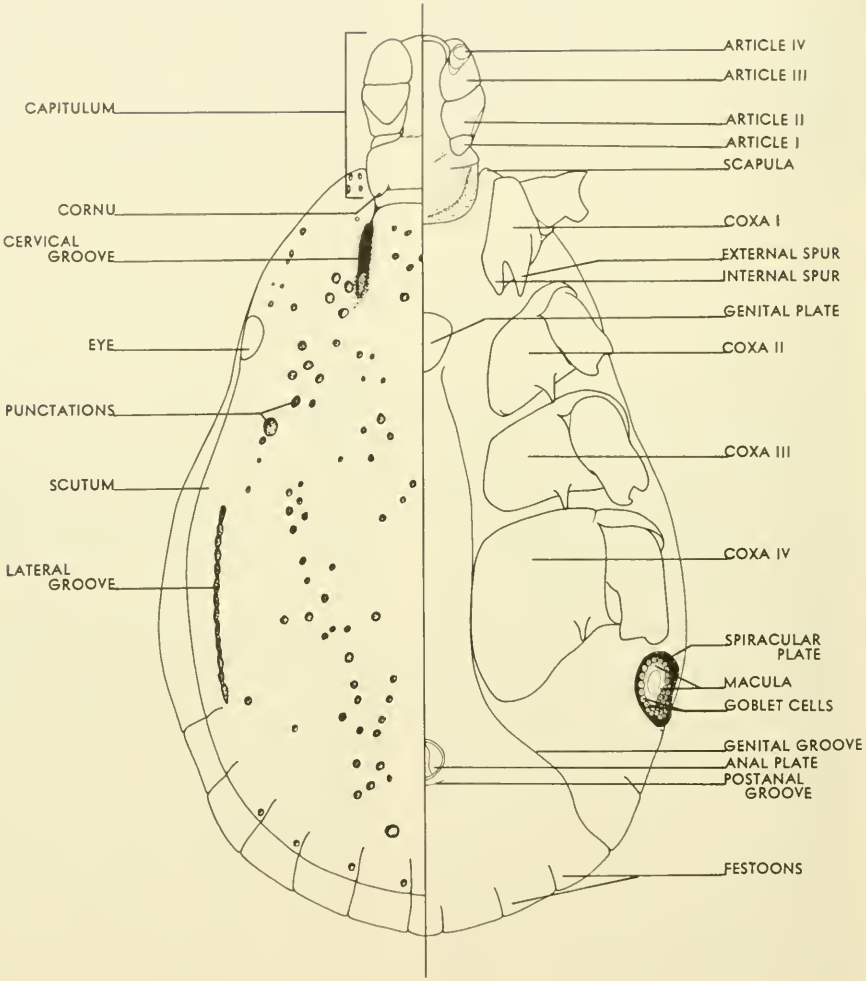


Fig. 1. Dorsal and ventral views, male *Dermacentor*.

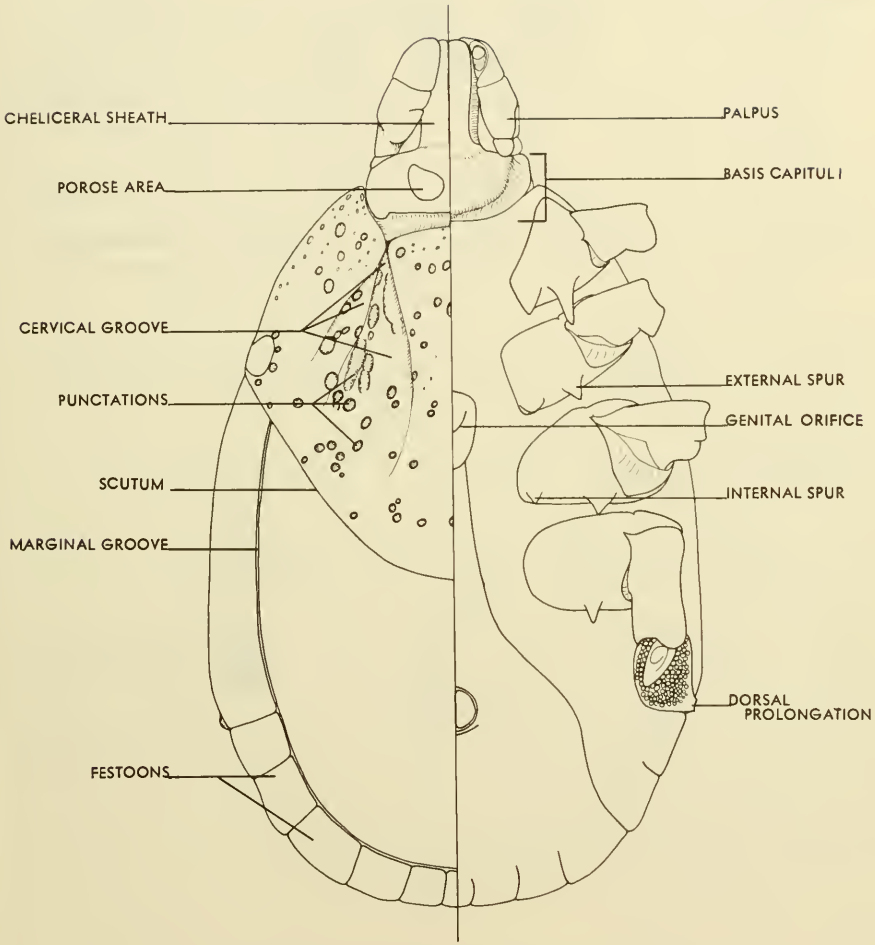


Fig. 2. Dorsal and ventral views, female *Dermacentor*.

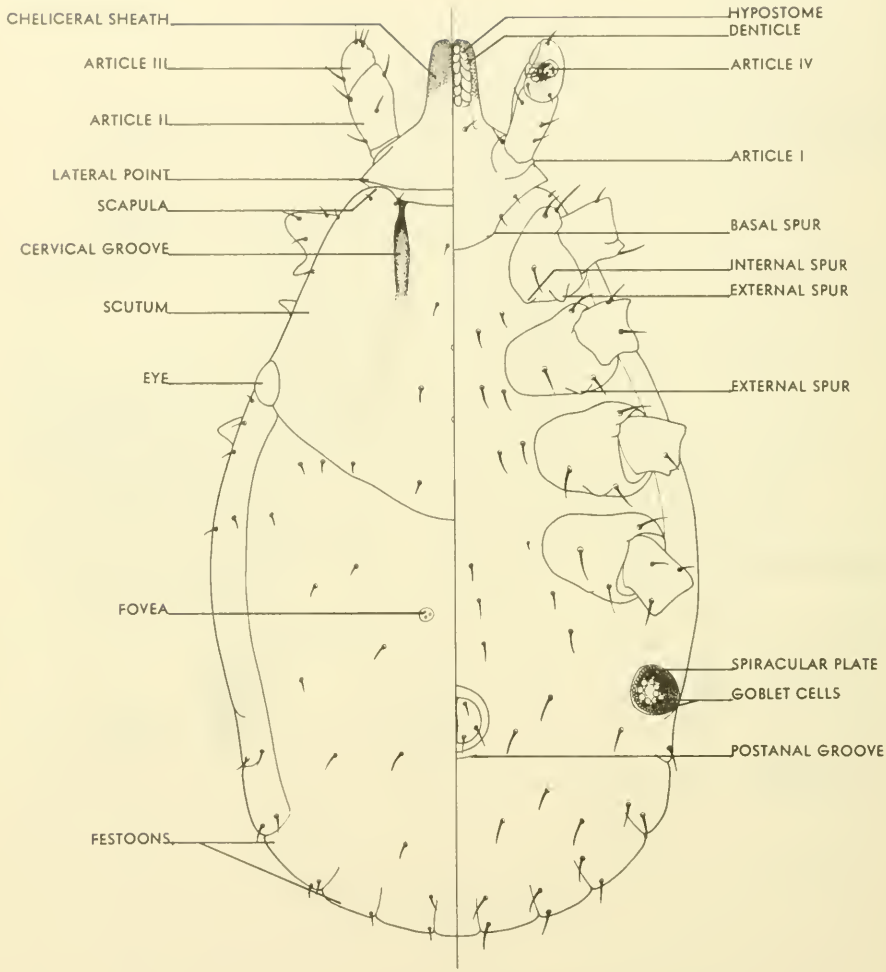


Fig. 3. Dorsal and ventral views, nymphal *Dermacentor*.

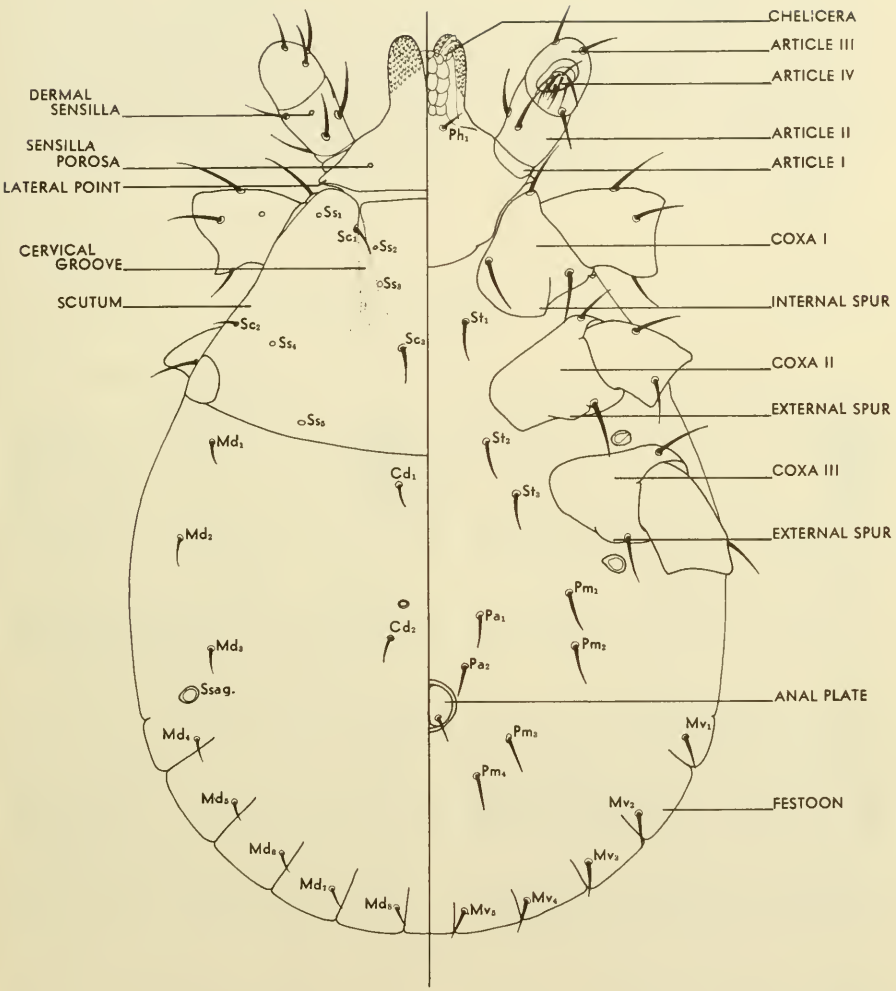


Fig. 4. Dorsal and ventral views, larval *Dermacentor*.
Abbreviations of setal nomenclature: *Cd*, central dorsal; *Md*, marginal dorsal; *Mv*, marginal ventral; *Pa*, preanal; *Ph*, posthypostomal; *Pm*, premarginal; *Sc*, scutal; *Ss*, scutal sensilla; *Ssag.*, sensilla sagittiformia; *St*, sternal.

Measurements of the length of ticks are exclusive of the capitulum, i.e., from the apex of the scapula to the median-posterior margin. Measurements are given in millimeters and were made on unengorged specimens. Mean scutal length was compared against the mean idiosomal length to get a per cent mean scutal length for each species in the larval stage.

General terminology used to designate anatomical and morphological features for this study is that of Cooley (1938). Setal terminology in the labelled drawing of the larval stage is after Clifford and Anastos (1960). The term *dermal sensilla* is after Cerny (1957). The terms *sensilla porosa* and *scutal sensilla* are after Robertson (1961). The terms *sensilla sagittiformia, sensilla haustiformia*, and *sensilla auriformia* are those used by Dinnik and Zumpt (1949) and Clifford and Anastos (1960).

RESULTS

General Observations

The general anatomical and morphological features which were emphasized as characteristics important to this study are described below.

Eyes are present in all developmental stages. Ornate scuta were observed only in the adult stage. Coloration is variable for both sexes within each species. Punctations are absent in the nymphal and larval stages.

Festoons are present in all stages. The adults and nymphs have eleven festoons and the larvae nine.

Hypostomes of all adults have dentition files of 3/3 in number. Hypostomes of the nymphs and larvae have dentition files of 2/2 in number. The number of denticles in a given file and the secondary dentition around the corona are variable within a given species. Hypostomal length varies according to the developmental stage, being longest in the adults.

Postanal grooves were observed in the adults and nymphs, but not in larvae. Genital grooves were observed in the males and females and a similar type groove was observed in the nymphs.

Figures 1, 2, 3, and 4 are labeled drawings of each sex and stage of development .

Detailed Species Description

There now follows a description, with illustrations, of features observed in each developmental stage for each species involved in this study. Only those characteristics are emphasized which for the most part are considered necessary to separate the species involved.

Dermacentor albipictus (Packard), 1869

Male (Figure 5)

Body: Idiosoma variable from a typical oval shape tapered at the anterior end to elliptical with weakly curved sides. An elongate form was observed to be more characteristic for this species than others. Length: Maximum, 6.2; minimum, 3.7; mean, 4.69. Width: Maximum, 3.8, minimum, 1.7; mean, 2.8.

Capitulum: Length greater than width. Palps having a short, broad, terminally blunt appearance. Basis capituli width greater than length. Cornua of moderate length yet prominent.

Scutum: Cervical grooves short, about twice as long as broad. Scutal punctations small, often indistinct but constant in size.

Coxae: Coxa I with elongate internal and external spurs, opposing margins of spurs parallel. External spurs present on coxae II, III, and IV, each being acute. Internal spurs present on coxae II and III, but sub-acute to indistinct.

Spiracular plate: Subcircular, with dorsal prolongation present or absent, broad and blunt when present. Goblet cells large and constant in size.

Female (Figure 6)

Body: Idiosoma ovate to sub-ovate with weakly curved sides, tapering slightly toward the anterior. Length: Maximum, 5.3; minimum, 3.2; mean, 4.45. Width: Maximum, 3.8; minimum, 2.0; mean, 2.63. Unengorged specimens from Montana largest, those from New Mexico smallest.

Capitulum: Length greater than width. Palps short, broad, and apically blunt. Basis capituli

Fig. 5. Dorsal and ventral views, male *Dermacentor albipictus.*

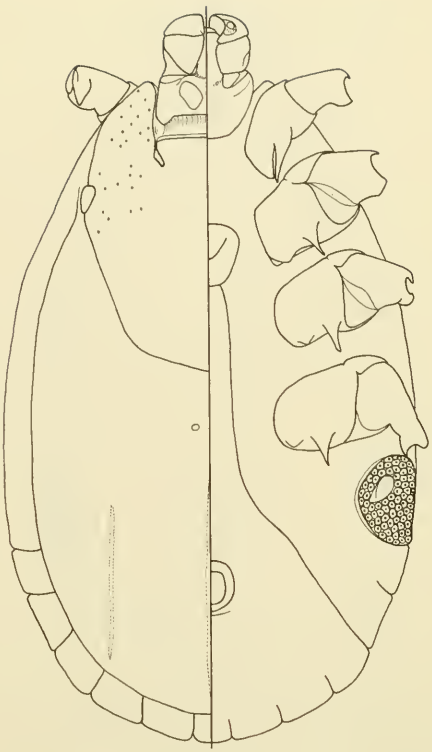


Fig. 6. Dorsal and ventral views, female *Dermacentor albipictus.*

width greater than length. Cornua sub-acute and distinct.

Scutum: Cervical grooves varying from short and rounded to moderately elongate. Punctations small and not numerous.

Coxae: Coxa I with elongate internal and external spurs, opposing margins parallel. External spurs present on coxae II, III, and IV. Internal spurs present on coxae II and III, small but distinct.

Spiracular plate: Sub-circular as in male, having large goblet cells of constant size. Dorsal prolongation present or absent, broad and blunt when present.

Nymph (Figure 7)

Body: Idiosoma distinctly elongate and slender. Lateral margins weakly curved. Length: Maximum, 2.3; minimum, 2.0; mean, 2.15. Width: Maximum, 1.1; minimum, 0.8; mean, 0.95.

Capitulum: Short with short, broad, apically blunt palps. Basis capituli narrow having short, indistinct lateral points. Small, sub-acute cornua present. Basal spurs present.

Scutum: Elongate with a distinctly curved posterior margin. Cervical grooves long and narrow.

Coxae: Coxa I with an external spur of moderate size and an internal spur of small size. External spurs present on coxae II, III, and IV. Internal spurs absent on coxae II, III, and IV.

Spiracular plate: Large and broadly oval. Goblet cells large and distinct, from fifteen to twenty in number.

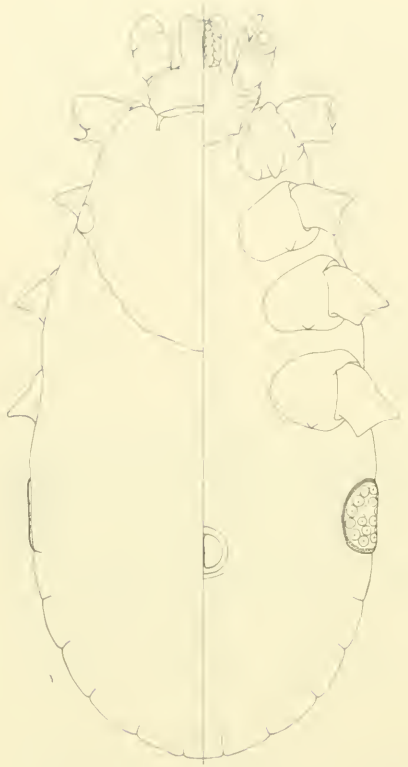


Fig. 7. Dorsal and ventral views, nymphal *Dermacentor albipictus.*

Larva (Figure 8)

Body: Idiosoma with lateral margins broadly oval. Length: maximum, 0.619; minimum, 0.572; mean, 0.592. Width: maximum, 0.538; minimum, 0.500; mean, 0.534.

Capitulum: Dorsal width greater than length. Palps broad and short. Basis capituli narrow. Lateral points indistinct. Sensilla porosa present.

Scutum: Per cent mean scutal length 46.5%. Prominently curved posterior margin. Cervical grooves elongate, with sides parallel. Scutal sensillae variable in their placement and may be present or absent.

Coxae: Coxa I with a sub-acute internal spur. Marginal, indistinct spurs on coxae II and III.

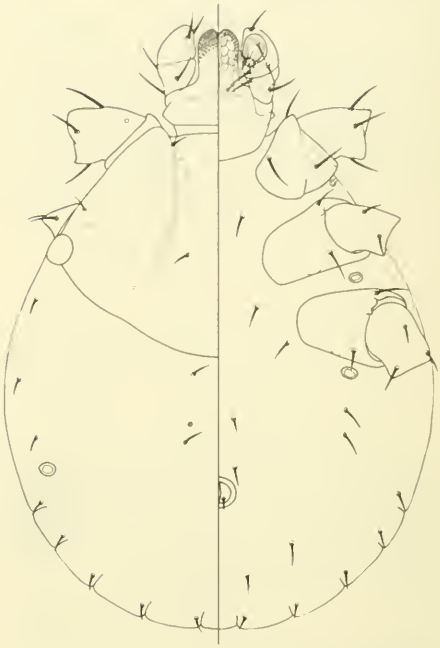


Fig. 8. Dorsal and ventral views, larval *Dermacentor albipictus.*

Dermacentor andersoni Stiles, 1908

Male (Figure 9)

Body: Idiosoma typically oval, tapering anteriorly. Genital plate distinct. Length: Maximum, 5.5; minimum, 2.6; mean, 4.71. Width: Maximum, 3.7; minimum, 1.65; mean 2.57.

Capitulum: Distinctly longer than wide, generally rectangular. Palps of moderate width, apically sub-acute. Basis capituli width greater than length. Cornua of moderate length and sub-acute.

Scutum: Extending entire length of idiosoma. Punctations moderate to large and distinct. Cervical grooves three times as long as broad. Lateral groove short or incomplete.

Coxae: Coxa I with opposing margins of internal and external spurs parallel. External spur slender. External spurs of coxae II, III, and IV longer than wide and acute. Internal spurs on coxae II and III present, but very reduced. Coxa IV large and posteriorly elongate, in some

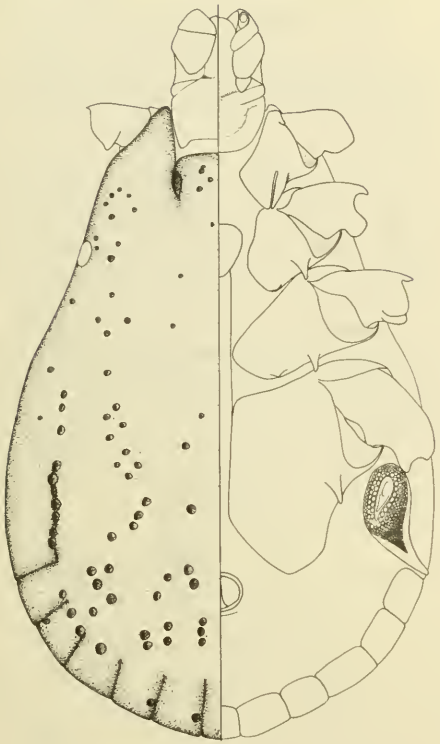


Fig. 9. Dorsal and ventral views, male *Dermacentor andersoni.*

Fig. 10. Dorsal and ventral views, female *Dermacentor andersoni.*

specimens extending to level of the anterior margin of anal plate.

Spiracular plate: Oval, with a long, slender dorsal prolongation of variable width. Macula variable in size and shape. Goblet cells of moderate size around macula, becoming progressively smaller toward the periphery of the plate.

Female (Figure 10)

Body: Idiosoma broad with a distinctly curved lateral margin. Length: Maximum, 4.9; minimum, 3.0; mean, 3.58. Width: Maximum, 2.75; minimum, 1.9; mean, 2.15.

Capitulum: Length slightly greater than width. Palps moderate in width and extending anterior to the hypostome, apically rounded. Basis capituli width greater than length. Cornua broad sub-apically. Porose areas large and distinct.

Scutum: Punctations vary from small to large, distributed beyond posterior margin of scutum. Posterior margin of scutum irregularly curved. Cervical grooves elongate.

Coxae: Coxa I with opposing margins of external and internal spurs parallel. External spur longer than the internal. External spurs present on coxae II, III, and IV, the width greater than length. Internal spurs present on coxae II and III, marginal and sub-acute.

Spiracular plate: Oval to sub-oval in outline, with distinct dorsal prolongation. Goblet cells of moderate size around macula, becoming smaller toward periphery of the plate. Macula large and variable in shape.

Nymph (Figure 11)

Body: Idiosoma elongate, lateral margins broadly curved. Length: Maximum, 1.45; minimum, 1.3; mean, 1.33. Width: Maximum, 0.95; minimum, 0.80, mean, 0.90.

Fig. 11. Dorsal and ventral views, nymphal *Dermacentor andersoni.*

Capitulum: Width greater than length. Lateral points of basis capituli prominent, extending beyond apex of scapula. Anterolateral edge of basis irregularly curved. Palps apically rounded. Basal spurs prominent.

Scutum: Posterior margin prominently curved. Cervical groove long and narrow, proximal margins not parallel.

Coxae: Coxa I with external spur large and internal spur moderately small and prominent. External spurs variable in size. External spurs present on coxae II, III, and IV, marginal and sub-acute. Internal spurs absent.

Spiracular plate: Large and sub-circular. A ring of moderately large goblet cells around the macula, remaining goblet cells of moderate size.

Larva (Figure 12)

Body: Idiosoma oval, tapering anteriorly. Lateral edges prominently curved. Length: Maximum, 0.662; minimum, 0.624; mean, 0.642. Width: Maximum, 0.543; minimum, 0.460; mean, 0.504.

Capitulum: Dorsal width greater than length. Palps of moderate width and apically sub-acute. Dermal sensilla present on article II. Lateral points distinct. Anterolateral edge irregularly curved. Posterodorsal margin of basis curved.

Scutum: Per cent mean scutal length 38.7%. Cervical grooves extending posteriorly half the distance of the scutum. Four pairs of scutal sensillae. Presence or absence of scutal sensillae variable.

Coxae: Internal spur on coxa I semi-acute. Broad sub-acute spurs present on coxae II and III, marginal or post-marginal.

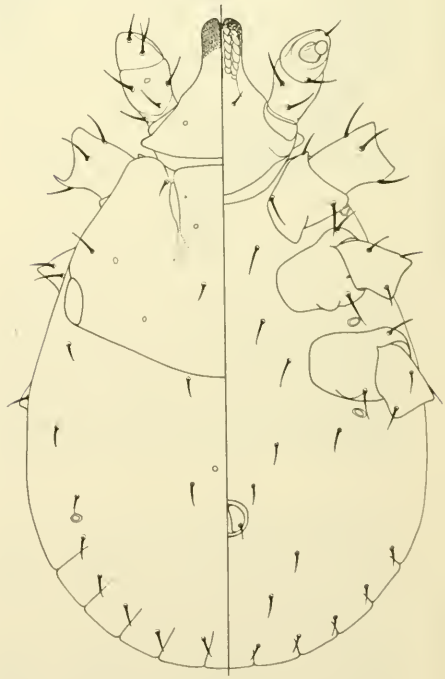


Fig. 12. Dorsal and ventral views, larval *Dermacentor andersoni.*

Dermacentor halli McIntosh, 1931

Male (Figure 13)

Body: Idiosoma broadly oval. Length: Maximum, 3.7; minimum, 3.4; mean, 3.56. Width: Maximum, 2.6; minimum, 2.3; mean, 2.47.

Capitulum: Dorsal length equal to width. Palps short and broad, apically rounded or blunt. Basis capituli distinctly broader than long, small punctations present. Cornua of moderate length and acute.

Scutum: With small punctations. Cervical grooves short and rounded. Lateral groove not well defined.

Coxae: Coxa I with internal and external spurs present. Opposing margins of spurs divergent. External spurs acute on coxae II, III, and IV. Internal spurs present on coxae II and III, marginal and rounded. Coxa IV moderately small.

Spiracular plate: Of medium size and oval, having small goblet cells. Dorsal prolongation of moderate width and length. Macula small.

Female (Figure 14)

Body: Idiosoma broadly oval, lateral edges distinctly curved. Marginal groove distinct in unengorged specimens. Length: Maximum, 4.1; minimum, 3.9; mean, 4.07. Width: Maximum, 2.65; minimum, 2.6; mean 2.62.

Capitulum: Dorsal width equal to length. Palps short and broad, apically sub-acute. Basis capituli width greater than length, lateral edges curved. Cornua short and sub-acute.

Scutum: Long and broad, extending posteriorly approximately half the distance of the idiosoma. Punctations small, sparse and located anteriorly on the scutum. Cervical grooves twice as long as broad.

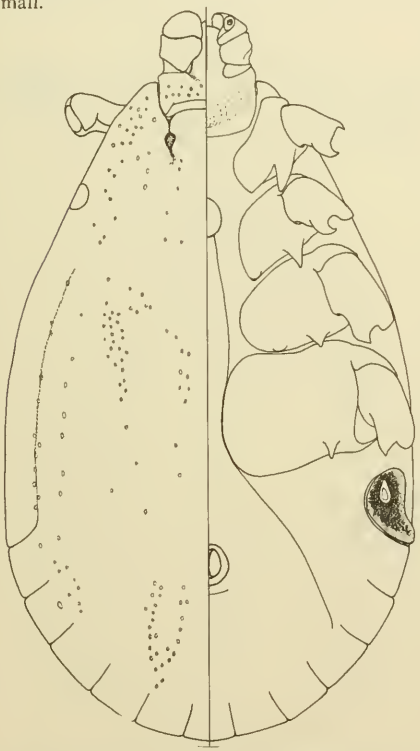


Fig. 13. Dorsal and ventral views, male *Dermacentor halli.*

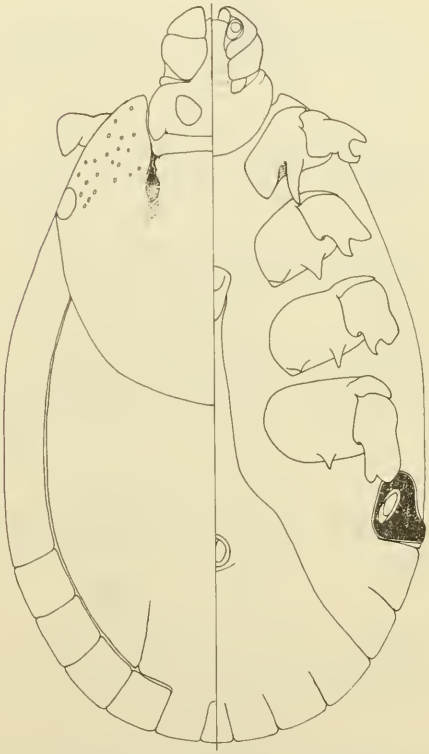


Fig. 14. Dorsal and ventral views, female *Dermacentor halli.*

Coxae: Coxa I with internal and external spurs, opposing margins of spurs divergent. External spur distinctly longer than internal spur. External spurs present on coxae II, III, and IV, acute. Internal spurs sub-acute, present on coxae II and III, absent on IV.

Spiracular plate: Oval and somewhat flattened. Macula moderately large and variable in form. Goblet cells uniformly small over entire plate. Dorsal prolongation of moderate width and length.

Nymph (Figure 15)

Body: Idiosoma long and slender, lateral margins weakly curved, tapering anteriorly. Length: Maximum, 1.3; minimum, 1.3; mean, 1.3. Width: Maximum, 0.75; minimum, 0.70; mean, 0.725.

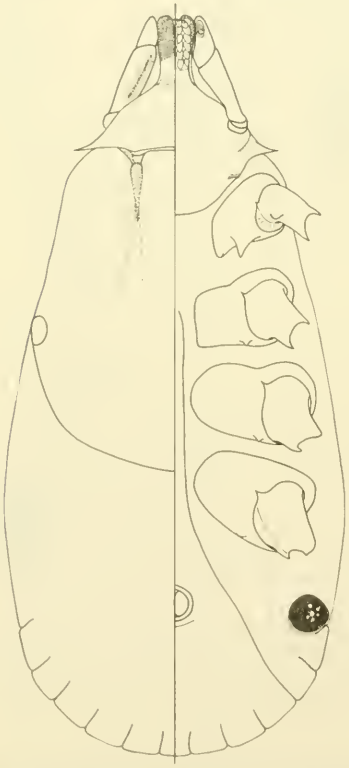


Fig. 15. Dorsal and ventral views, nymphal *Dermacentor halli*.

Capitulum: Dorsal width greater than length. Hypostome slender. Palps long and slender. Basis capituli with distinctly elongate, acute lateral points. Cornua absent. Anterolateral margin of basis broadly convex. Basal spurs marginal and sub-acute.

Scutum: Distinctly elongate, extending posteriorly over half the distance of the idiosoma. Cervical grooves long, proximal margins not parallel.

Coxae: Coxa I with external spur broad at base and apically acute. Internal spur indistinct. Small external spurs present on coxae II and III. External spur on coxa IV reduced to a relatively indistinct marginal rounded elevation.

Spiracular plate: Small and sub-circular, with a small, blunt dorsal prolongation. Several medium-sized goblet cells adjacent to the small round macula. Remaining goblet cells small.

Larva (Figure 16)

Body: Idiosoma oval in shape, tapering anteriorly. Length: Maximum, 0.705; minimum, 0.581; mean, 0.642. Width: Maximum, 0.654; minimum, 0.480; mean, 0.563.

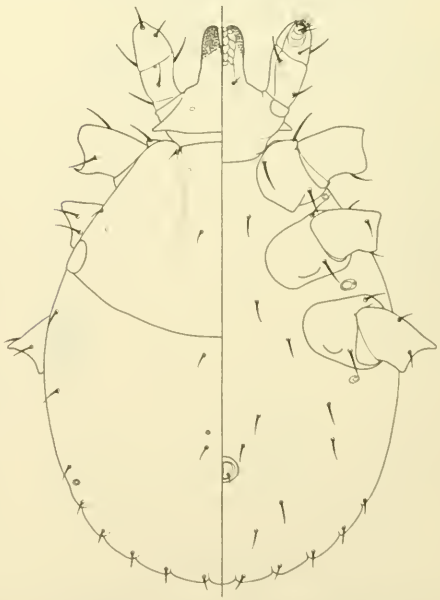


Fig. 16. Dorsal and ventral views, larval *Dermacentor halli*.

Capitulum: Dorsal width greater than length. Palpal apex sub-acute. Dermal sensilla present. Basis capituli with lateral points moderately slender yet distinctly acute, extending beyond apex of scapulae. Sensilla porosa present.

Scutum: Broadly curved posterior margin. Per cent mean scutal length 47.7%. Cervical grooves long and narrow. Scutal sensillae variable in number.

Coxae: Coxa I with a broad, sub-acute spur. Coxae II and III with sub-marginal spurs.

Dermacentor hunteri Bishop, 1912

Male (Figure 17)

Body: Idiosoma distinctly broad posteriorly and laterally, tapering anteriorly. Festoons large. Length: Maximum, 4.3; minimum, 3.85; mean, 4.09. Width: Maximum, 2.8; minimum, 2.5; mean, 2.66.

Fig. 17. Dorsal and ventral views, male *Dermacentor hunteri*.

Capitulum: Dorsal length greater than width. Palps of moderate width and apically blunt. Basis capituli width greater than length. Cornua of moderate length, semi-acute.

Scutum: Punctations small and constant in size. Cervical groove short, twice as long as wide. Lateral groove indistinct.

Coxae: Coxa I with opposing margins of internal and external spurs parallel. Coxae II, III, and IV with external spurs semi-acute. Internal spurs on coxae II and III very much reduced. Coxa IV moderately large.

Spiracular plate: Oval, with a slender dorsal prolongation. Goblet cells around macula moderately large, medium-sized in the dorsal prolongation. Macula large and variable in shape.

Female (Figure 18)

Body: Idiosoma oval with tapering anterolateral margin. Marginal groove distinct in unengorged specimens. Length: Maximum, 4.0; minimum, 3.6; mean, 3.7. Width: Maximum, 2.8; minimum, 2.1; mean, 2.4.

Capitulum: Width greater than length. Palps extending beyond hypostome and rounded apically. Basis capituli with lateral edges curved, width greater than length. Cornua broad and sub-acute.

Scutum: Distinctly tapered posteriorly, extending half the length of the idiosoma. Punctations variable in size. Cervical grooves short, twice as long as broad.

Coxae: Coxa I with opposing margins of internal and external spurs parallel. Internal spur longer than the external. External spurs on coxae II, III, and IV as wide at base as long. Internal spurs present on coxae II and III, wider than long.

Spiracular plate: Oval in shape with a moderately broadened dorsal prolongation. Goblet cells moderately large, smaller in the dorsal prolongation. Macula variable in size and shape.

Nymph (Figure 19)

Body: Posterolateral margin of idiosoma broadly curved. Anterolateral margin slightly curved and tapering. Length: Maximum, 1.55; minimum, 1.45; mean, 1.47. Width: Maximum, 1.2; minimum, 1.0; mean, 1.09.

Capitulum: Width at widest point equal to length. Anterolateral margin of basis capituli

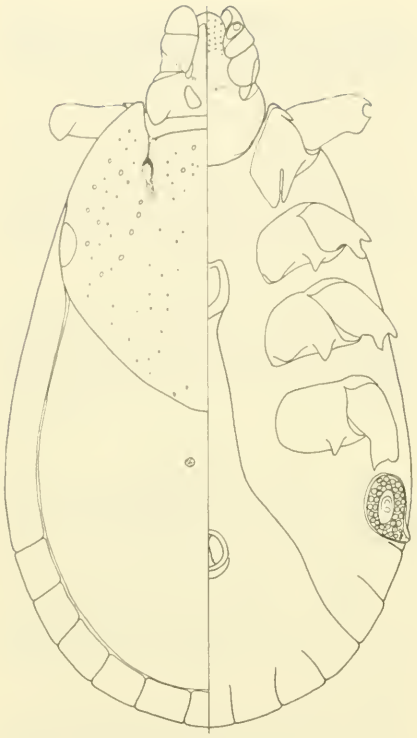


Fig. 18. Dorsal and ventral views, female *Dermacentor hunteri.*

Fig. 19. Dorsal and ventral views, nymphal *Dermacentor hunteri.*

irregularly curved. Basis with lateral projection extending beyond apex of scapula.

Scutum: Short, extending posteriorly one-third the idiosomal length. Length of cervical grooves approximately six times greater than width.

Coxae: Coxa I with external spur as broad at base as long. Internal spur on coxa I small, indistinct; marginal when present. External spurs on coxae II, III, and IV, marginal, rounded and small.

Spiracular plate: Oval, sub-acutely tapered dorsally. Goblet cells small compared to those of the adult. A ring of slightly larger goblet cells surround the macula.

Larva (Figure 20)

Body: Idiosoma with posterior and mid-lateral margins broadly curved, anterolateral margin tapered. Idiosoma sub-circular. Length: Maximum, 0.638; minimum, 0.516; mean, 0.595. Width: Maximum, 0.540; minimum, 0.475; mean, 0.501.

Capitulum: Width at lateral points greater than length. Palps broad and apically rounded. Dermal sensilla and sensilla porosa absent. Lateral point of basis capituli extending beyond apex of scapulae. Anterolateral margin of basis irregularly curved.

Scutum: Per cent mean scutal length 35.3%. Length about one-third that of idiosoma. Posterior margin only slightly curved. Cervical grooves with margins divergent.

Coxae: Coxa I with a broad sub-acute internal spur. Coxae II and III with broad post-marginal external spurs.

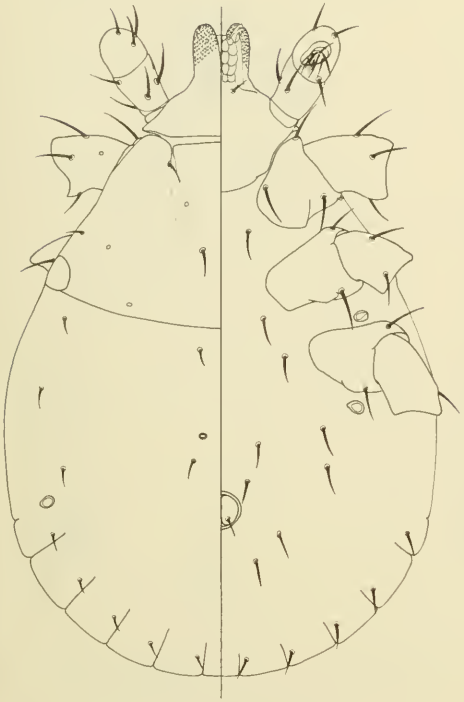


Fig. 20. Dorsal and ventral views, larval *Dermacentor hunteri*.

Dermacentor occidentalis Marx, 1892

Male (Figure 21)

Body: Idiosoma elongate and oval. Lateral margins prominently curved, tapering anterolaterally. Length: Maximum, 3.8; minimum, 2.7; mean, 3.3. Width: Maximum, 2.5; minimum, 1.85; mean, 2.25.

Capitulum: Dorsal width as great as length. Palps short and broad and apically blunt. Basis capituli width greater than length. Cornua elongate, apically varying from blunt to pointed.

Scutum: Punctations uniform in size, tending to be small. Cervical grooves short, rounded and pit-like. Lateral groove indistinct.

Coxae: Coxa I with opposing margins of internal and external spurs parallel. Spurs large and prominent. External spurs present on coxae II, III, and IV, acute. Internal spurs present on coxae II and III, broadly curved. Coxa IV variable in size, in some cases extending posteriorly to level of anal plate.

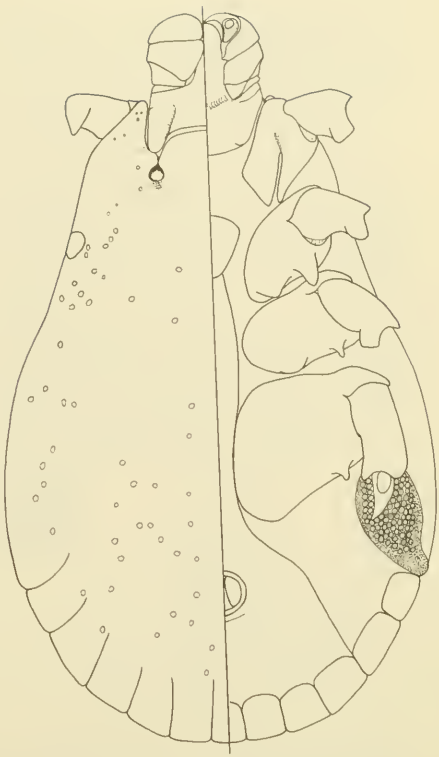


Fig. 21. Dorsal and ventral views, male *Dermacentor occidentalis*.

Spiracular plate: Large and oval with dorsal prolongation moderately broad and blunt. Goblet cells distinct, not extending to apex of dorsal prolongation. Macula large, variable in shape.

Female (Figure 22)

Body: Idiosoma oval and tapering at the anterolateral margin. Marginal groove distinct in unengorged specimens. Length: Maximum, 3.6; minimum, 2.6; mean, 3.2. Width: Maximum, 2.3; minimum, 1.7; mean, 2.06.

Capitulum: Dorsal width equal to length. Palps short, apically blunt. Basis capituli distinctly broader than long. Cornua large but not as elongate as in the male. Porose areas broadly oval.

Scutum: Extending posteriorly approximately half the length of the idiosoma. Punctations

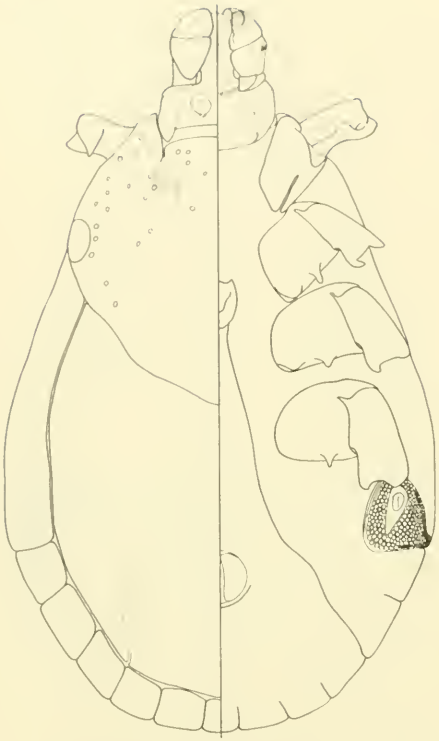


Fig. 22. Dorsal and ventral views, female *Dermacentor occidentalis*.

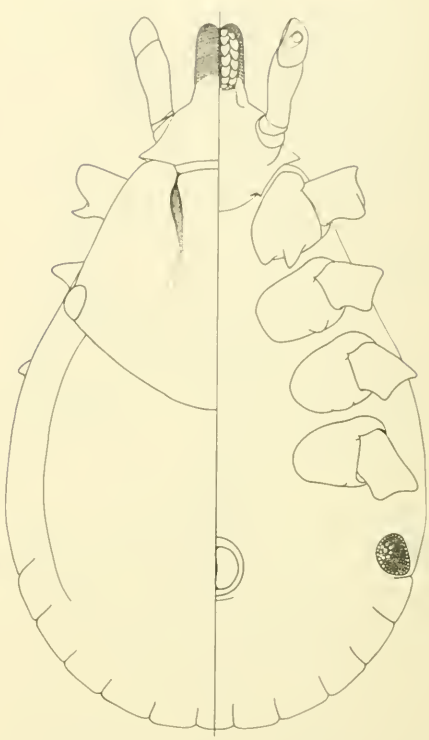


Fig. 23. Dorsal and ventral views, nymphal *Dermacentor occidentalis*.

few yet distinct and constant in size. Cervical grooves short, broad and shallow, extending fan-like posteriorly.

Coxae: Coxa I with opposing margins of internal and external spurs parallel. External spurs on coxae II, III, and IV, acute to sub-acute. Internal spurs present on coxae II and III, marginal and broadly rounded.

Spiracular plate: Inner and posterior margins straight. Short dorsal prolongation present. Goblet cells of moderate size, slightly smaller than in the male. Macula large.

Nymph (Figure 23)

Body: Idiosoma oval, anterolateral margins evenly tapering. Lateral groove present in unengorged specimens. Length: Maximum, 1.2; minimum, 1.05; mean, 1.10. Width: Maximum, 0.9; minimum, 0.75; mean, 0.82.

Capitulum: Dorsal width slightly greater than length. Palps long and slender. Basis capituli with lateral points extending beyond apex of scapulae. Anterolateral margin of basis irregularly curved. Basal spurs postmarginal.

Scutum: Extends posteriorly one-third to one-half the length of the idiosoma. Cervical grooves long, deepened anteriorly. Posterior margin curved. Punctations absent.

Coxae: Coxa I with a medium-sized external spur and a marginal internal spur. External spurs present on coxae II and III. A slight marginal projecting external spur may be present or absent on coxa IV.

Spiracular plate: Essentially oval, broadly curved ventrally and tapering dorsally to a distinct apex. Goblet cells moderately small. Ring of slightly larger goblet cells adjacent to the orifice. Macula absent.

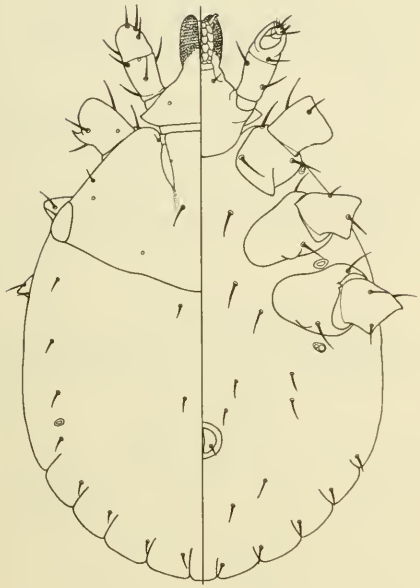


Fig. 24. Dorsal and ventral views, larval *Dermacentor occidentalis.*

Larva (Figure 24)

Body: Idiosoma oval. Lateral margins distinctly curved. Length: Maximum, 0.634; minimum, 0.529; mean, 0.582. Width: Maximum, 0.582; minimum, 0.437; mean, 0.466.

Capitulum: Width slightly greater than length. Palps of moderate width and length, apically rounded and equal to length of hypostome. Basis capituli with lateral points extending beyond apex of scapulae. Posterodorsal margin of basis straight to slightly concave.

Scutum: Per cent mean acutal length 41.3%. Extends posteriorly over one-third the length of the idiosoma. Cervical grooves extend half the length of the scutum. Scutal sensilla present.

Coxae: Coxa I with internal spur semi-acute. External spurs compressed and broadened on coxae II and III.

Dermacentor parumapertus Neumann, 1901

Male (Figure 25)

Body: Idiosoma elongate, oval and lateral margins may be irregularly curved. Length: Maximum, 2.9; minimum 2.6; mean, 2.72. Width: Maximum, 1.9; minimum, 1.6; mean, 1.71.

Capitulum: Length greater than width, and rectangular. Palps of moderate length and apically rounded. Basis capituli width greater than length. Cornua short, wider than long and apically rounded.

Scutum: May or may not extend entire length and width of idiosoma. Some punctations large, interspersed among slightly smaller punctations which predominate. Cervical grooves of moderate length, deepened anteriorly. Proximal margins of grooves parallel. Short lateral grooves present at posterior half of body.

Coxae: Coxa I with opposing margins of internal and external spurs divergent. External spurs present on coxae II, III, and IV. Internal spurs absent on coxae II, III, and IV; however, indistinct marginal elevations may be present on coxae II and III in some specimens.

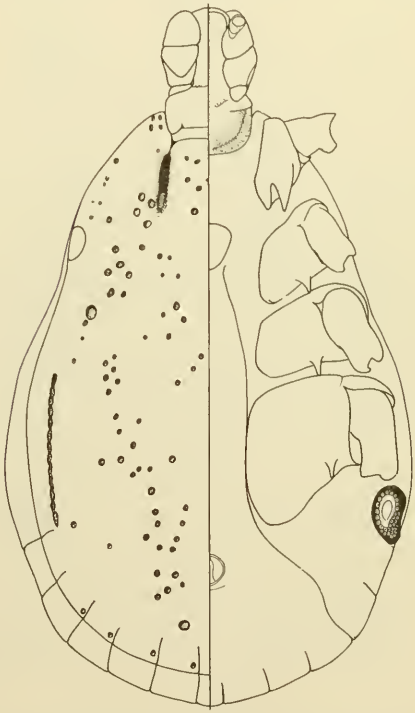


Fig. 25. Dorsal and ventral views, male *Dermacentor parumapertus.*

Spiracular plate: Moderately small, oval, with a broad dorsal prolongation. Size of goblet cells variable with those adjacent to the macula slightly larger. Macula large, variable in size and shape.

Female (Figure 26)

Body: Idiosoma broadly oval with the lateral margins curved. Length: Maximum, 3.15; minimum, 3.1; mean, 3.13. Width: Maximum, 2.15; minimum, 2.0; mean, 2.08.

Capitulum: Length slightly greater than width. Palps moderately long and equal to length of hypostome. Basis capituli broad and short. Lateral margins distinctly curved. Cornua width greater than length, short and blunt. Porose areas prominent and sub-circular.

Scutum: Extends half the length of the idiosoma in unengorged specimens. Posterior margin distinctly curved. Cervical grooves elongate, divergent, widening very much posteriorly. Large punctations predominate in numbers over smaller, more moderately sized punctations. Punctations confluent in the area of the cervical grooves.

Coxae: Coxa I with opposing margins of internal and external spurs divergent. External spurs present on coxae II, III, and IV. Internal spurs present only on coxae II and III.

Spiracular plate: Broadly oval, with a distinct dorsal prolongation. Goblet cells relatively constant in size.

Nymph (Figure 27)

Body: Idiosoma elongate, oval, with lateral margins irregularly curved. Length: Maximum,

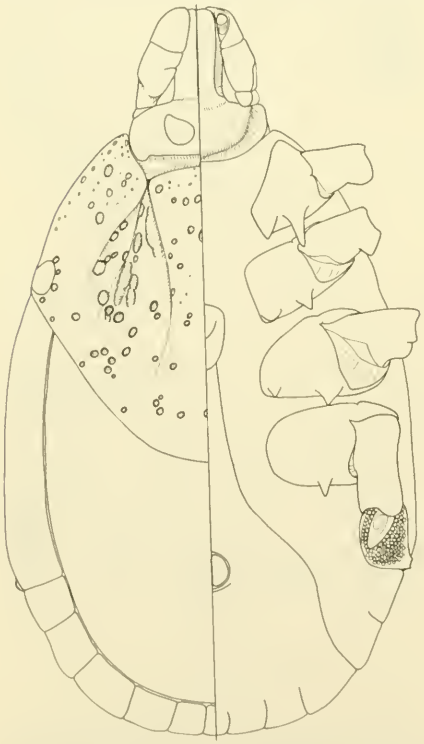


Fig. 26. Dorsal and ventral views, female *Dermacentor parumapertus.*

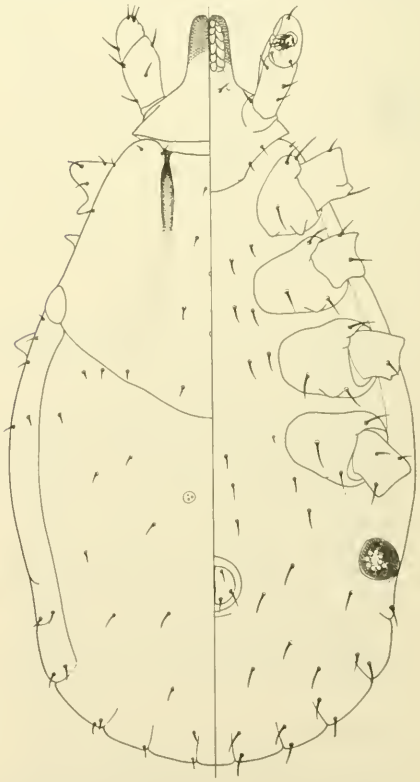


Fig. 27. Dorsal and ventral views, nymphal *Dermacentor parumapertus.*

1.45; minimum, 1.14; mean 1.3. Width: Maximum, 1.0; minimum, 0.75; mean, 0.86.

Capitulum: Width slightly greater than length. Palps moderately long, extending slightly beyond apex of hypostome. Anterolateral margin of capitulum irregularly curved. Basis capituli with lateral points extending beyond apex of scapulae. Posterodorsal margin of basis straight.

Scutum: With posterior margin distinctly arcuate. Cervical grooves long, posteriorly shallow, anteriorly deepened, with opposing margins parallel. Scutum extends over one-third the length of the idiosoma.

Coxae: Coxa I with external spur moderately small; internal spur indistinct in some specimens. External spurs present on coxae II, III, and IV, rounded, marginal and small. Internal spur on coxa IV difficult to discern in some specimens.

Spiracular plate: Sub-circular with dorsal prolongation very short to none at all. Goblet cells uniformly small, except for a ring of slightly larger cells surrounding the macula.

Larva (Figure 28)

Body: Idiosoma broadly oval. Length: Maximum, 0.754; minimum, 0.662; mean, 0.707. Width: Maximum, 0.605; minimum, 0.509; mean, 0.571.

Capitulum: Width greater than length. Palps moderately broad and apically rounded. Dermal sensilla present. Basis capituli with moderately short lateral points. Anterolateral margin irregularly curved.

Scutum: Per cent mean scutal to idiosomal length 36.3%. Posterior margin broadly arcuate. Scutum extends posteriorly one-third the idiosoma length. Cervical grooves of moderate length, opposing margins parallel.

Coxae: Coxa I with internal spur broad and sub-acute. Broad, slightly elevated external spurs on coxae II and III. Internal spurs absent.

Dermacentor variabilis (Say), 1821

Male (Figure 29)

Body: Idiosoma elongate and oval. Lateral margins irregularly curved anteriorly, posterior margin rounded. Length: Maximum: 4.4; minimum, 3.5; mean, 3.9. Width: Maximum, 2.85; minimum, 2.3; mean, 2.42.

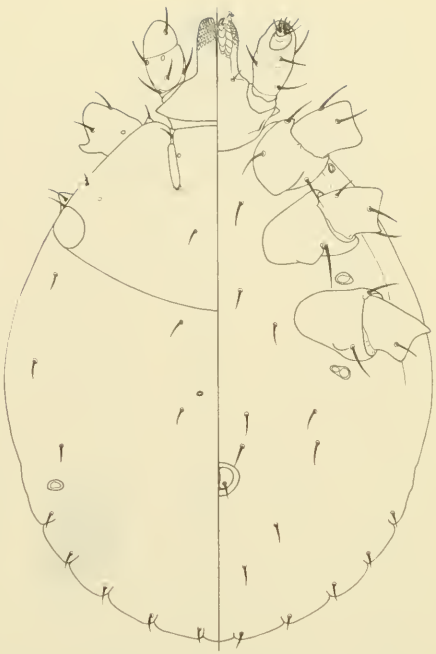


Fig. 28. Dorsal and ventral views, larval *Dermacentor parumapertus.*

Capitulum: Length greater than width. Palps short, broad, and apically rounded. Cornua of moderate length and blunt. Basis capituli width exceeding length.

Scutum: Widely scattered large and small punctations. Due to size the larger punctations indicate dominance in numbers but the smaller punctations actually are greater in numbers. Cervical grooves moderately deep, short, with pit-like posterior depressions.

Coxae: Coxa I with opposing margins of internal and external spurs parallel. Coxae II, III, and IV with acute external spurs. Internal spurs broadly curved on coxae II and III.

Spiracular plate: Large and broadly curved inwardly, straight outwardly. Dorsal prolongation variable in length and width. Goblet cells minute and constant in size. Macula variable in shape.

Female (Figure 30)

Body: Idiosoma elongate and oval. Lateral margins irregularly curved anteriorly with pos-

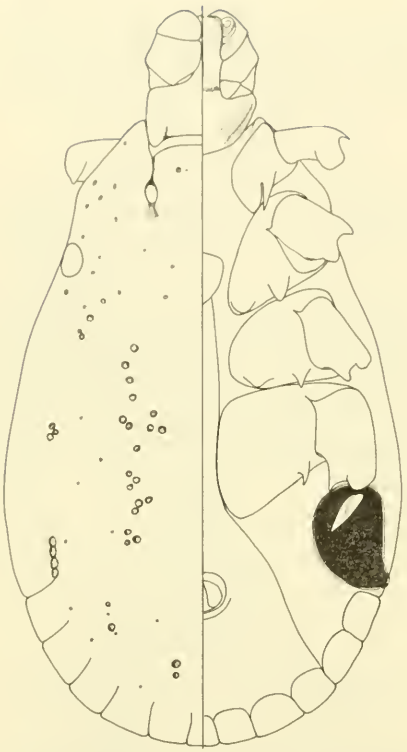


Fig. 29. Dorsal and ventral views, male *Dermacentor variabilis.*

Fig. 30. Dorsal and ventral views, female *Dermacentor variabilis.*

terior margin evenly rounded. Marginal groove distinct in unengorged specimens. Length: Maximum, 4.3; minimum, 3.65; mean, 3.96. Width: Maximum, 2.95; minimum, 2.3; mean, 2.57.

Capitulum: Length greater than width. Palps apically blunt. Basis capituli width greater than length. Cornua short and apically rounded. Porose areas bean-shaped.

Scutum: Large punctations predominate in numbers over small punctations. Punctations extend beyond the posterior margin of the scutum. Scutum extends half the distance of the idiosoma. Cervical grooves narrow and pit-like anteriorly. Posterior margin of scutum sharply arcuate.

Coxae: Coxa I with opposing margins of internal and external spurs parallel. External spurs present on coxae II, III, and IV, with basal width equal to length. Internal spurs present, marginal, blunt, and apically rounded on coxae II and III, absent on coxa IV.

Spiracular plate: Large and sub-circular. Goblet cells numerous, minute and uniform size. Macula oval and large. Dorsal prolongation distinct and elongate.

Nymph (Figure 31)

Body: Idiosoma ovulate posterior, anteriorly elongate and tapering. Length: Maximum, 1.5; minimum, 1.4; mean, 1.44. Width: Maximum, 1.0; minimum, 0.9; mean 0.94.

Capitulum: Width equal to length. Palps long and slender. Anterolateral margin of basis capituli straight to weakly concave. Lateral points of basis long and slender, extending well

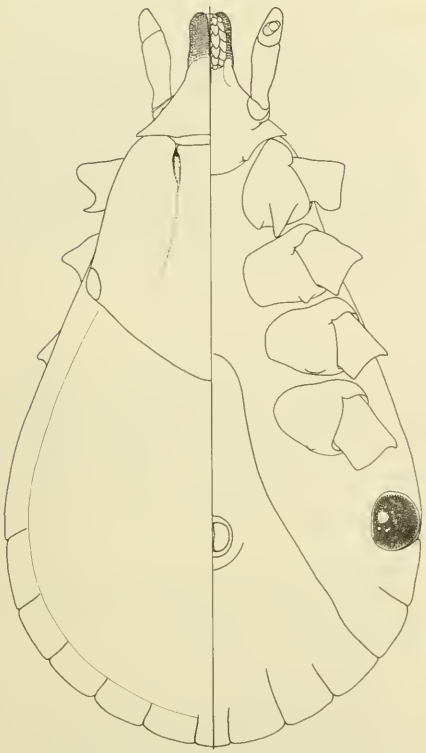


Fig. 31. Dorsal and ventral views, nymphal *Dermacentor variabilis*.

beyond apex of scapulae. Posterodorsal margin of basis essentially straight. Basal spurs subacute and distinct.

Scutum: Posterior margin distinctly arcuate, extending from one-third to one-half the length of the idiosoma. Cervical grooves elongate and slender.

Coxae: External spur on coxa I semi-acute, large. Internal spur small and relatively indistinct. External spurs present on coxae II, III, and IV, but somewhat indistinct especially on coxa IV.

Spiracular plate: Sub-circular, with inner margin straight. Goblet cells minute, numerous, and uniform in size. There may be a ring of slightly larger goblet cells surrounding the macula.

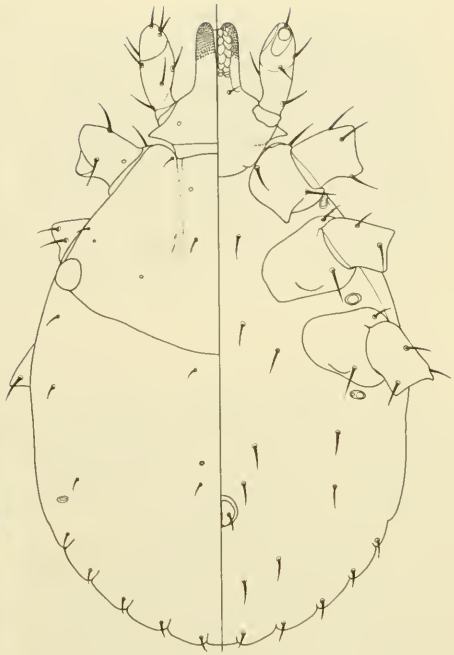


Fig. 32. Dorsal and ventral views, larval *Dermacentor variabilis*.

Larva (Figure 32)

Body: Idiosoma elongate with lateral margins distinctly curved. Length: Maximum, 0.656; minimum, 0.582; mean, 0.628. Width: Maximum, 0.518; minimum, 0.504; mean, 0.509.

Capitulum: Dorsal length greater than width. Palps somewhat slender. Dermal sensilla absent. Anterolateral margin of basis capituli irregularly curved. Lateral points of basis prominent. Posterodorsal margin of basis straight.

Scutum: Per cent mean scutal length 38.9%. Posterior margin slightly irregular. Cervical grooves shallow, with margins parallel. Scutum extends posteriorly one-third to one-half the length of the idiosoma.

Coxae: Coxa I with a broadly based, distantly acute internal spur. Sub-marginal, broad external spurs present on coxae II and III may appear as slight elevations or wrinkles.

DISCUSSION

The following discussion is presented in three units referrable to the adults, nymphs, and larvae. In each instance there is a general discussion of anatomical and morphological features as observed in this study for all the species in each stage of development. Concluding each separate discussion is an illustrated key for the identification of the species.

The anatomical and morphological characteristics used in the illustrated keys for the adults and nymphs are essentially those applied by Cooley (1938) and Arthur (1960) with some minor modifications. In the larvae a number of features were selected by the writers and others from a number of sources. It has been necessary in some instances in all stages of development to resort to the use of geographical distribution, altitudinal differences, host-parasite relationships, and other features as a means of taxonomic separation.

ADULTS

Body: Idiosomal lengths and widths in general are in agreement with those of Cooley (1938). All species conform to a general oval shape posteriorly with tapered anterolateral margins. Some variation in body outline was observed in females, which may be due perhaps to the lack of the scutum not covering the dorsum as in the male. Nevertheless body size was variable both within species and between species. Male specimens of *D. albipictus* from Montana are the largest ticks observed. Some are over 6.0 mm in length. Specimens of *D. albipictus* from Utah averaged 4.5 mm in length. Those from New Mexico averaged 3.7 mm in length. Similar variation in length was found in unengorged females of this species from the same localities. Variation in size was also noted in other species, but there was nothing so consistent and dramatically different as observed in *D. albipictus*.

The most variable body features observed between the species are palpal length and width, length of cornua and shape, spiracular plate shape and size, number and size of goblet cells which are described as being large, small, and minute. There are variations also in size, distribution, and number of dorsal punctations. This is also true of the size and shape of the cervical grooves. All of these features, however, are relatively constant within any given species and seem to be reliable features which may be used taxonomically.

The distribution, numbers, and size of setae were found to be most variable in the adult stage. For these reasons it was decided that chaetotaxy is too unreliable to use in separating the species, at least for *Dermacentor* in the western United States.

Capitulum: Two general forms were observed in the capitula of the adults. It is square in *D. albipictus*, *D. halli*, and *D. occidentalis*, and rectangular (wider from side to side than anterior-posteriorly) in *D. andersoni*, *D. parumapertus*, *D. hunteri*, and *D. variabilis*. Some exceptions between the sexes were noted. For instance the *D. variabilis* male has a somewhat square capitulum, while the female is rectangular.

Scutum: Coloration observed in the adults is variable in both sexes and within each species, so it is not useful for our purposes. For description of coloration in *Dermacentor* ticks see Cooley (1938).

While shallow and deep grooves on the idiosoma could generally be distinguished, sufficient variation exists to prohibit their use as key characteristics. General size and shape of the cervical grooves, however, were found to be constant. Punctations in both sexes are always separate and distinct, except for the female of *D. parumapertus* where some of the large punctations are confluent.

Length of the scutum in the females is more or less constant in relation to the overall length of the idiosoma. In general, the posterior margin extends posteriorly from one-third to one-half the idiosomal length in unengorged specimens.

Coxae: In general the greatest variation in the coxal size was found in coxa IV of the males. *D. albipictus* from Montana has a distinctly larger coxa IV than specimens of the same species from New Mexico. This was readily measured by noting the distance from the anal plate to the posterior apex of coxa IV. Coxa IV on *D. andersoni* from western Colorado is the largest observed for all species. It extends posteriorly to the level of the anterior margin of the anal plate. A similar situation was found with *D. occidentalis*. Coxa IV in *D. variabilis* and *D. halli* is the smallest observed in males.

Coxa IV in the females is constant for any given species. Coxae I, II, and III also are generally constant for any given species. There is a good deal of variation in position, number, shape and size of coxal spurs between species, but relatively constant for each species.

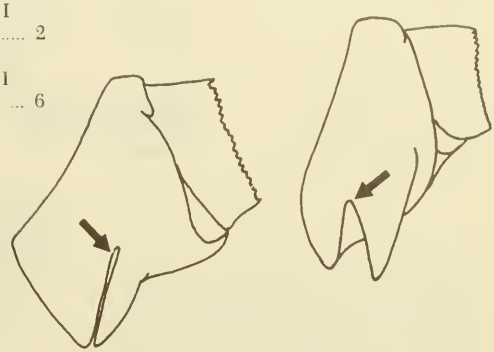
D. parumapertus and *D. halli* have the proximal margins of the spurs on coxa I divergent. In *D. halli* this divergence is apparently constant. In *D. parumapertus* the divergence varies, with specimens from Idaho, Wyoming, northern Utah, and northern Nevada being narrowly divergent, and specimens from the southern part of Utah and Nevada being broadly divergent.

External spurs are consistently present on all four coxae. Internal spurs are present on coxae I, II, and III and absent on coxa IV. The length and width of the internal spurs vary markedly, from marginal rounded elevations to acute spurs. On the other hand, external spurs are more constant in form. Variation in length and width does exist, however.

Key for the Identification of Species of *Dermacentor* Males

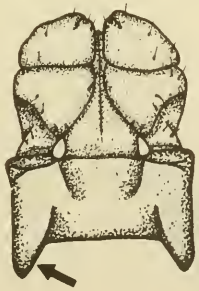
1. Opposing margins of spurs on coxa I parallel 2

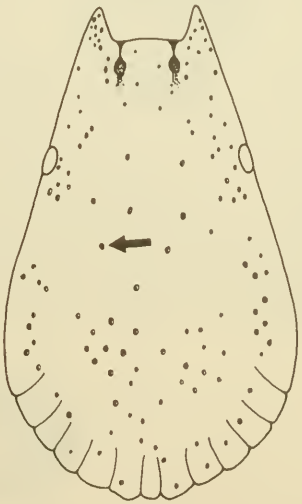
   Opposing margins of spurs on coxa I not parallel 6



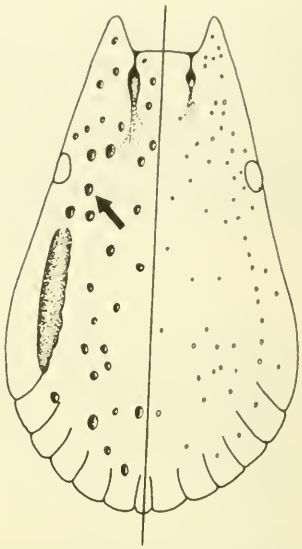
2. Cornua about twice as long as broad. Scutal punctations noticeably small. Cervical grooves short, terminally rounded and pit-like ..... *D. occidentalis* (See figure 21)

   Distribution along the Pacific coastal plain, mainly in central and northern California, western Oregon, and in southwestern Washington.



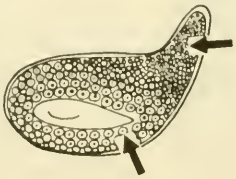


Corona less than twice as long as broad. Mixture of large and small punctations on scutum. Comparative size of punctations shown in couplet illustration. Cervical grooves usually elongate and pitlike. Lateral grooves deep and elongate when present 3



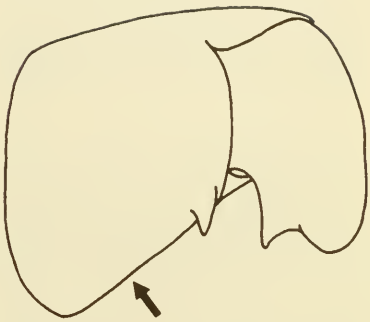
3. Coxa IV large, posterior margin almost at the level of the anterior margin of the anal plate. External spur on coxa IV longer than wide. Goblet cells of medium size, pore visible and distinct, cells becoming smaller toward periphery of spiracular plate and especially the dorsal prolongation ..... *D. andersoni* (See figure 9)

Most common (*Dermacentor*) tick of larger vertebrates in the region of its distribution which is in the higher elevations of the Great Basin states; northern Arizona, northern New Mexico, western Colorado, all of Utah, Nevada, northeastern California; and from the mountain and lowland areas of eastern Oregon, eastern Washington, Idaho, Wyoming, Montana and western Canada. In higher elevations of Great Basin states it is the most common tick parasite of the porcupine. This is the common "Wood Tick" which as an adult attacks man, many of his domestic animals, and larger native vertebrates. The next most abundant tick in the same regions of distribution is *Dermacentor albipictus*.

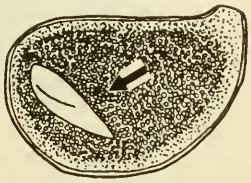


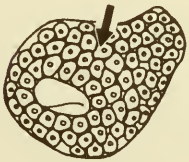
Goblet cells of uniform size in the central area of the spiracular plate. They are either very small, giving a granular texture to the plate, or very large, with goblet pore distinct. Posterior margin of coxa IV does not extend to anterior level of anal plate. Basal width of external spur on coxa IV as broad as long 4

4. Goblet cells very small and granular-like. General shape of coxa IV square. External spur on coxa IV stout and blunt .... *D. variabilis* (See figure 29)

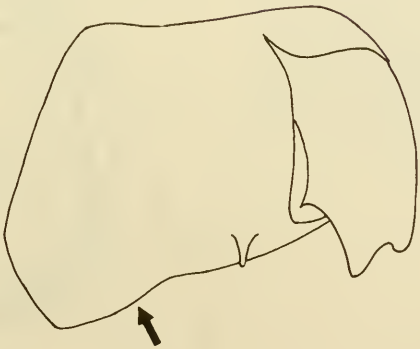


In the western U. S., distribution is limited to the north and central coastal plains region of California and extreme southwestern Oregon. Occasional collections may be made in other parts of western U. S., but these will most likely be taken from dogs in transit from the eastern U. S. where this species is most common and widely distributed.



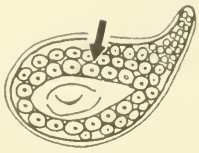


Goblet cells very large, pores very distinct. Spiracular plate variable in shape. Coxa IV longer than broad 5



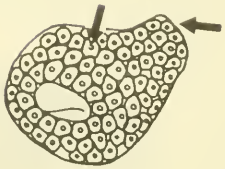
5. Dorsal prolongation of spiracular plate narrow. Goblet cells in the neck of the prolongation smaller than those around the macula ..... *D. hunteri* (See figure 17)

The principal host is the Desert Bighorn sheep. Mule deer in the range of the Desert Bighorn sheep also host this tick. Two collections have been taken from lagomorphs and several from man. Distribution at present restricted to higher elevations. Desert Bighorn sheep range in mountain areas of New Mexico, Arizona, and southern Nevada. They may be found at lower elevations (2500-3500 feet above sea level) in migrating from one range to another. Specimens found on man and lagomorphs in southwestern Utah and southeastern Nevada were about 3000 feet above sea level.



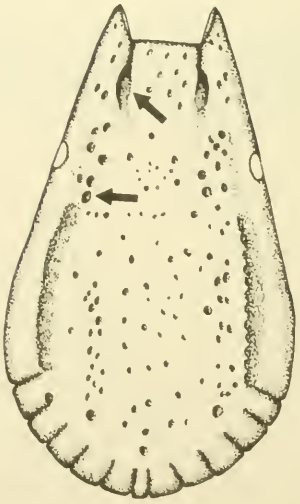
Dorsal prolongation of spiracular plate broad and short to absent. Goblet cells very large and constant in size with pores distinct. Goblet cells the largest of any species of *Dermacentor* in western U. S. ..... *D. albipictus* (See figure 5)

So far the only known single-host *Dermacentor* tick in the western U. S. It is a common parasite of deer and elk at higher elevations in the Great Basin states, and of larger vertebrates such as moose, horse, elk, antelope, Rocky Mountain sheep and deer in the northern tier of states in the western U. S. and in Canada.



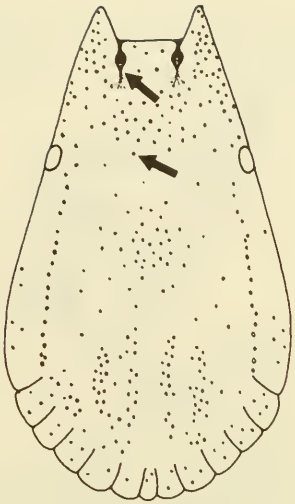
6. Scutal punctations a mixture of large and small with the smaller predominating in number. Cervical grooves three to four times longer than broad, deepened anteriorly and open posteriorly. Lateral grooves distinct at posterior half of body ..... *D. parumapertus* (See figure 25)

Known from lowlands of southern Idaho, southeastern Oregon, east of the coastal ranges in California, lowlands of Nevada, Utah, Colorado, Arizona, New Mexico, western Texas, western Oklahoma, and northern Mexico. The California Black-tailed jackrabbit is the most common host and it is very unusual to collect adult ticks of this species on other hosts.



Scutal punctations small and uniform in size. Cervical grooves short, deep and pit-like. Lateral grooves relatively indistinct. Goblet cells small, similar to *D. variabilis* ..... *D. halli* (See figure 13)

At present known only from south-central Texas and Central America. Apparenlty the peccary is the principal host.

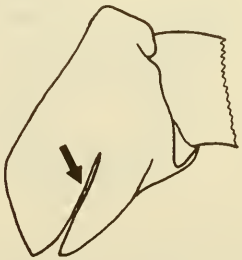


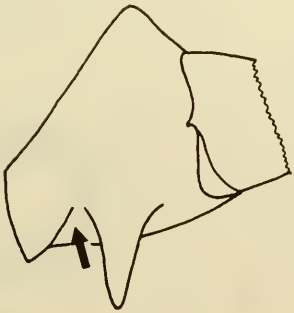
Key for the Identification of Species of *Dermacentor* Females

In each couplet where the species is listed, refer to geographic distribution information and host parasite relationships described in the key of identification for the males of *Dermacentor*.

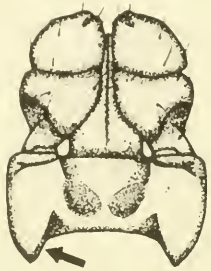
1. Opposing margins of spurs on coxa I parallel 2

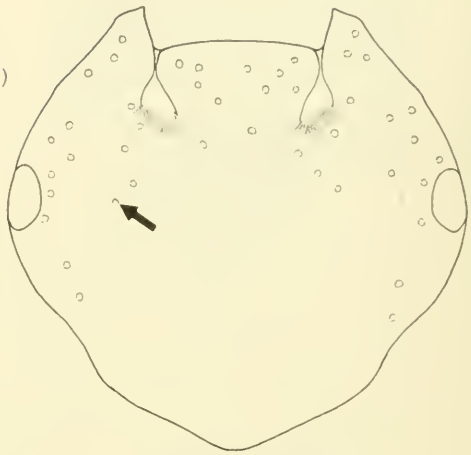
   Opposing margins of spurs on coxa I divergent 6



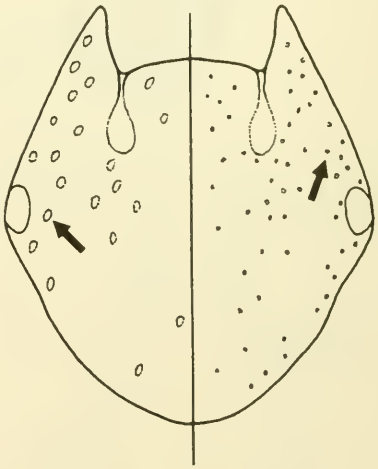


2. Cornua as long as broad. Scutal punctations sparsely scattered, shallow but of the same size. Cervical grooves short, shallow and expanding fan-like posteriorly *D. occidentalis* (See figure 22)

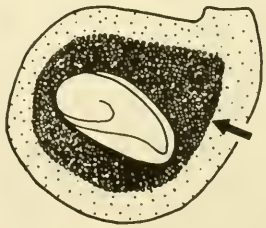




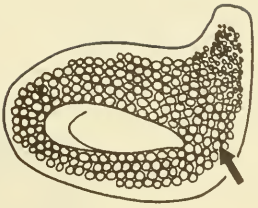
Cornua broader than long. Scutal punctations mixed in size, large to minute. (See couplet illustration for comparative sizes.) Cervical grooves elongate but distally closed. Porose areas large and ovulate 3



3. Spiracular plate with goblet cells so minute as to display a granular texture, most densely concentrated around the macula. Porose areas usually bean-shaped .... *D. variabilis* (See figure 30)

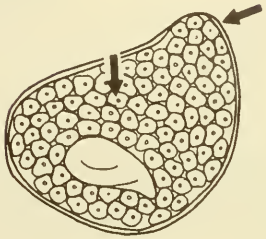


Spiracular plate with medium to very large goblet cells 4

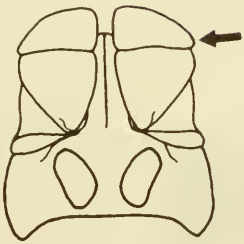


4. Goblet cells of medium size, usually smaller in the dorsal prolongation, which is long and narrow ..... *D. andersoni* (See figure 10)

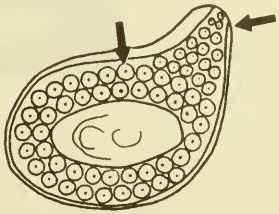
Spiracular plate with large, evenly distributed goblet cells. The pores of the goblet cells very distinct 5

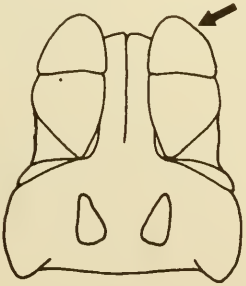


5. Spiracular plate with very large goblet cells, constant in size. Dorsal prolongation of spiracular plate broad truncate, or lacking. Palps with article III twice as wide as long ..... *D. albipictus* (See figure 6)

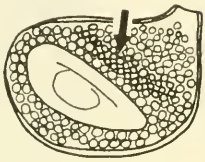


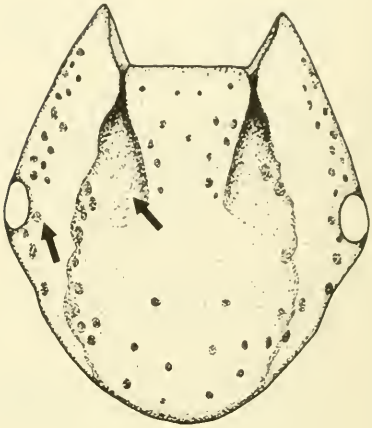
Spiracular plate with large goblet cells but not constant in size, those in the dorsal prolongation slightly smaller. Dorsal prolongation elongate and always present. Palps usually elongate, article III as long as broad ..... *D. hunteri* (See figure 18)



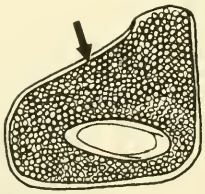


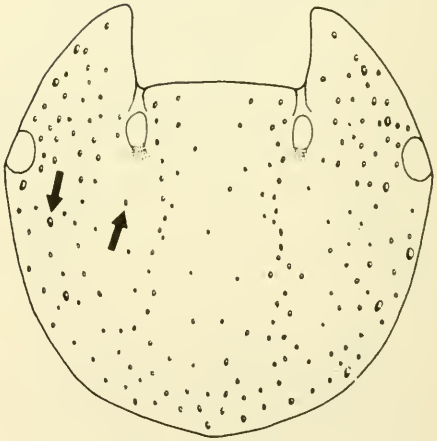
6. Spiracular plate with goblet cells medium and constant in size. Punctations on scutum large. Cervical groove long, deep and expanding posteriorly ..... *D. parumapertus* (See figure 26)





Spiracular plate with goblet cells minute in size. Scutum with small punctations except at periphery, where they are slightly larger. Cervical groove short and shallow ..... *D. halli* (See figure 14)





Nymphs

The number and placement of setae in the nymphs are too variable to be of use in separating the species considered in this study.

The lateral points of the basis capituli in *D. albipictus* are the shortest observed in all species. The lateral points on the basis capituli of *D. halli* are the longest of all species examined. The lateral points of *D. halli* and *D. variabilis* extend well beyond the apex of the scapulae.

Palpal length and width are variable between species. Short, broad palps were observed in *D. albipictus* while long, slender palps were found in *D. occidentalis* and *D. variabilis*.

Basal spurs are present on all species with the exception of *D. hunteri*. They are most distinct on *D. occidentalis*.

Scutum: Punctations and ornamentation are absent in the nymphal stage. Size of scutum is distinctly variable. *D. halli* has the largest and *D. hunteri* the smallest. The curvature of the posterior margin is also variable among the species with *D. halli* having a broadly curved, almost truncate margin. *D. hunteri* is weakly curved. No particular form of cervical groove can be described as typical.

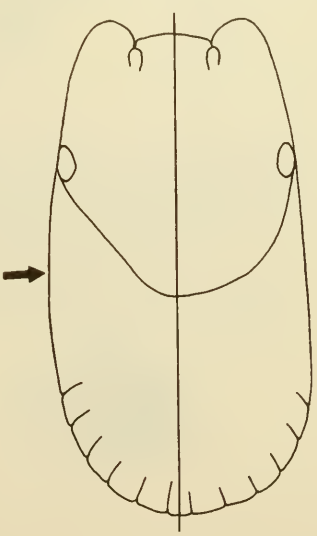
Coxae: The external spur on coxa I is distinct in each species. *D. andersoni* has the largest with *D. variabilis* possessing the next largest. *D. parumapertus* has the smallest spur for coxa I. The external spur on coxa IV of *D. occidentalis* and *D. parumapertus* is indistinct to absent. The internal spur on coxa I is somewhat uniformly distinctive although it is essentially small in all the species.

Spiracular plate: A distinct variation was observed both in the size of plates and goblet cells. *D. albipictus* has the largest spiracular plate and goblet cells. *D. variabilis* has a relatively large plate, but the goblet cells are comparatively minute. *D. hunteri* has the smallest spiracular plate. In every species, with the exception of *D. albipictus*, a ring of larger goblet cells surrounds the spiracular opening. Variation in the number and placement of the ring of goblet cells is the rule. They are the largest in *D. andersoni* and next largest in *D. parumapertus*.

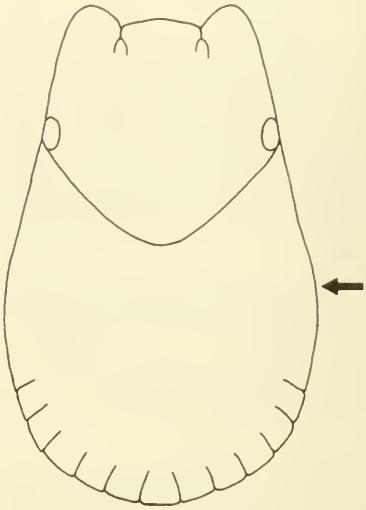
Key for the Identification of Species of *Dermacentor* Nymphs

Refer to geographic distribution and host parasite information as given for males for each species listed below.

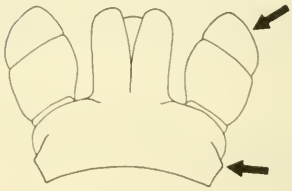
1. Idiosoma elongate and slender. Lateral margins weakly curved. Scutum variable in posterior marginal conformation, extending more than half the length of the idiosoma 2

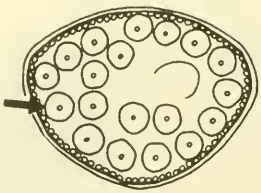


Idiosoma moderately broad. Lateral margins distinctly curved. Scutum extends less than one-half the length of the idiosoma 3

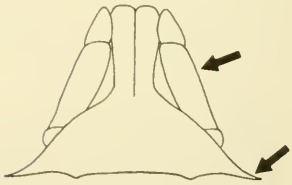


2. Basis capituli narrow, with lateral points small and poorly defined. Palps short, broad and apically blunt. Spiracular plate large and ovate. Goblet cells large ..... *D. albipictus* (See figure 7)

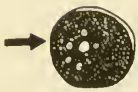




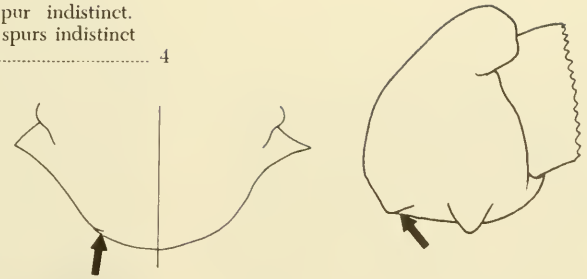
Basis capituli broad with lateral points distinct and sharp. Palps long and slender. Spiracular plate oval, goblet cells minute with a circle of slightly larger goblet cells centrally located ..... *D. halli* (See figure 15)



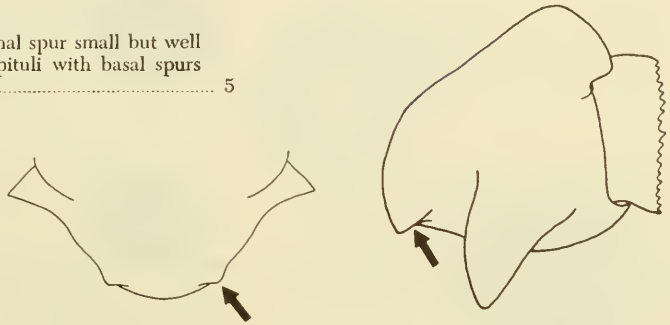
Little is known of the ecology of this species in nature. Life cycle data are known only from laboratory observations.



3. Coxa I with internal spur indistinct. Basis capituli with basal spurs indistinct or absent 4

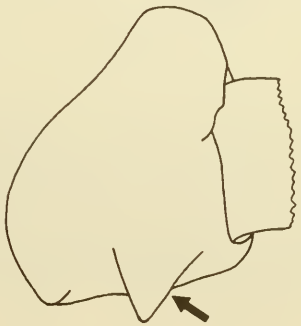


Coxa I with internal spur small but well defined. Basis capituli with basal spurs distinct 5



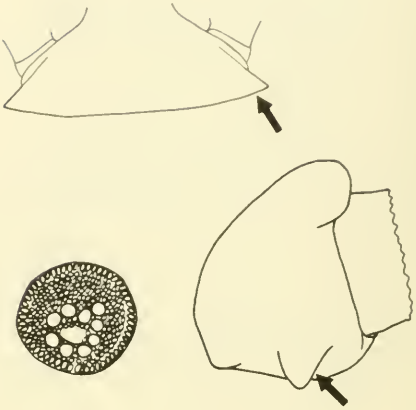
4. Basis capituli with lateral points moderately long, posterior border irregular. Anterolateral border slightly convex in outline. Coxa I with external spur as broad as long. Spiracular plate flatiron-like, with broad base inward. Goblet cells minute except for a ring of slightly larger goblet cells located around the macula ..... *D. hunteri* (See figure 19)

Life cycle data have been obtained from laboratory observations. Little is known of host parasite relationships of this species in nature.



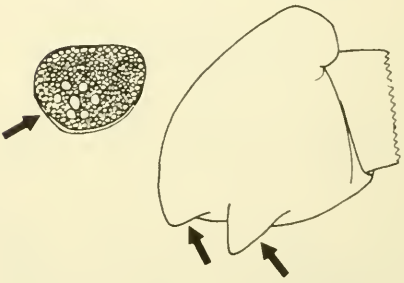
Basis capituli with lateral points of medium length, the anterolateral edge straight. Posterior border uniformly even. Coxa I with external spur moderately small and as broad as long. Spiracular plates rounded, with a ring of relatively large goblet cells clustered around the macula . ... *D. parumapterus* (See figure 27)

The nymphs of this species are found on small rodents such as kangaroo rats, several species of pocket mice, deer mice and ground squirrels located in the geographic areas where the adults are found. In general the largest host on which nymphs of this species are found is the Black-tailed jack rabbit.

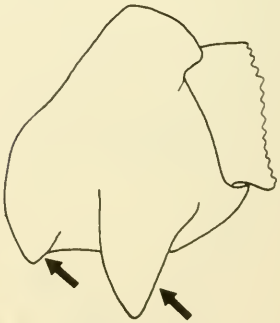


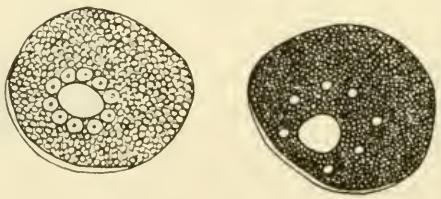
5. Spiracular plate small, ovoid, yet somewhat flattened inwardly. Coxa I with well-defined internal spur and an external spur which is located almost marginally. External spur about as broad as long ..... *D. occidentalis* (See figure 23)

Found on a number of species of smaller vertebrates.

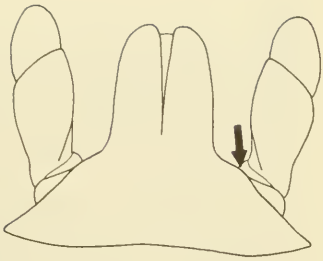


Spiracular plate large, ovoid, not depressed on inward surface. Goblet cells vary in size from minute to medium. (See couplet illustration.) Very distinct larger goblet cells situated ring-like around the macula. Coxa I with distinct internal and external spurs. The internal spur on coxa I is deflected outward 6

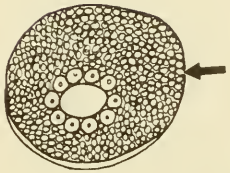




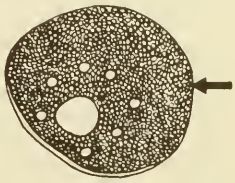
6. Basis capituli with anterolateral margin slightly elevated. Palps not slender. Goblet cells of moderate size. Large goblet cells closely associated with macula .... *D. andersoni* (See figure 11)



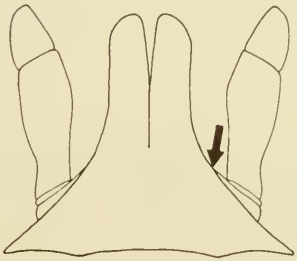
Nymphal stage found on smaller vertebrate species, mainly rodents typical of higher elevations. Such animals as tree squirrels, voles, deer mice, chipmunks, jumping mice, woodrats, prairie dogs and the marmot are common hosts. As one progresses toward more northern latitudinal geographic areas, the hosts for the nymphal stages vary. Nevertheless, there is a tendency for this species as nymphs to have a wide range in size of host selection, from marmots to deer mice.



Basis capituli with anterolateral margin slightly depressed. Palps slender (compared to *D. andersoni*). Goblet cells minute except for a ring of slightly larger goblet cells around the eccentrically located macula .... *D. variabilis* (See figure 31)



Although there are an abundance of data concerning the hosts of this species in the eastern and midwestern United States, the data are limited with reference to the western United States.



LARVAE

Body: General idiosomal form essentially oval for all species. Both length and width variable. *D. albipictus* is the most broad (subcircular). *D. parumapertus* has the greatest mean width and *D. occidentalis* has the narrowest. The posterolateral margins are distinctly rounded in all species.

Four pairs of sensilla sagittiformia are present, one pair posterior to each coxal plate (Ssag not shown on fig. 4 posterior to 1st coxal plate), and one dorsolateral pair on the opisthosoma. Due to their constant position they are of taxonomic value at least at the generic level. Various other sensillae were seen and studied. For example, sensilla haustiformia were observed on the scutum, postscutum, basis capituli, palps, and leg segments. Dermal sensilla, sensilla porosa, and the scutal sensillae are sensilla haustiformia according to Dinnink and Zumpt (1949). Nevertheless, only those sensillae observed on the palps, basis capituli and scutum are included in the drawings in this study. Further study on the comparative position of the sensilla haustiformia is needed to more fully determine their taxonomic utility at the species level.

The general arrangement of setae is relatively constant in all species studied. This is in agreement with Clifford and Anastos (1960). Because enough other characteristics are present to use for identification purposes, chaetotaxy was not emphasized.

Capitulum: *D. albipictus* has the narrowest basis capituli. Its lateral projections do not extend beyond the apex of the scapula. All other species in this study have distinct lateral points, extending beyond the scapular apex. The lateral points of *D. halli* are more tapered than in other species. The posterodorsal margin of the basis capituli and the lateral points are best observed on unmounted specimens. The capitulum naturally projects slightly downward and thus makes it difficult to observe these structures accurately on mounted specimens.

Palpal length and width are variable between species. *D. albipictus* has the shortest and widest palps, and *D. variabilis* has the longest and narrowest. The apices of the palps vary from rounded, as in *D. hunteri*, to sub-acute in *D. albipictus*. Dermal sensillae occur on all the species except *D. albipictus, D. hunteri*, and *D. variabilis*.

Scutum: In comparative per cent mean actual length *D. hunteri* has the shortest scutum, being 35.3% that of the idiosoma.

Commonly four pairs of scutal sensillae are present. Five pairs were infrequently seen and in some specimens only two or three were observed. Cervical grooves were observed on unmounted specimens at a magnification of 216 diameters, but were variable in shape.

Coxae: A single spur is present on each coxa in all species. Coxa I has an internal spur and coxae II and III external spurs. The spurs are generally constant in position, size, and shape for each species. The width or acuteness of the spur on coxa I is utilized as a taxonomic character in the key. Coxa I on *D. albipictus* is attached more anteriorly on the idiosoma than in the other species.

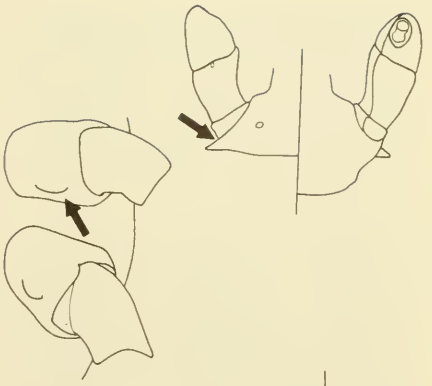
KEY FOR THE IDENTIFICATION OF SPECIES OF *Dermacentor* LARVAE

For use with mounted specimens, except where noted in the key.

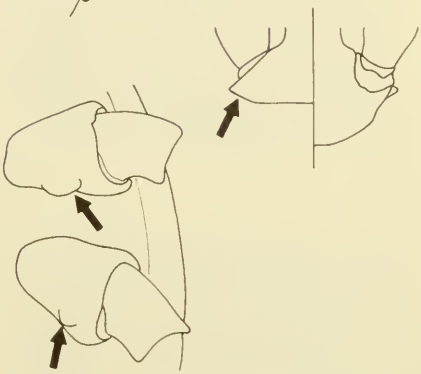
1. Dermal sensilla present 2
   Dermal sensilla absent 5

2. Lateral projections of basis capituli tapering narrowly, ending in acute lateral points (best observed on unmounted specimens). Spurs on coxae II and III submarginal ..... *D. halli* (See figure 16)

Known only from south-central Texas and Mexico. Very little is known of natural ecology.

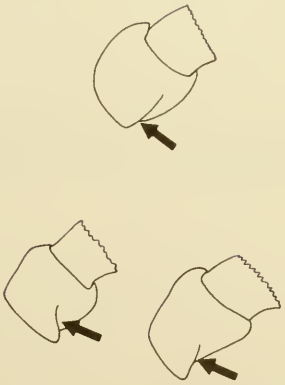


Lateral projections of basis capituli not narrowly tapering but ending subacutely. Spurs on coxae II and III marginal. (Couplet illustration shows dorsal and ventral views of basis capituli and lateral points.) Best observed in unmounted specimens 3



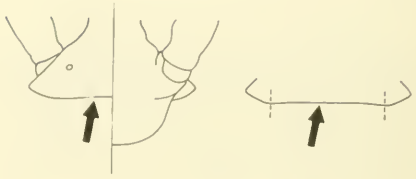
3. Spur on coxa I broadly tapered and subacute ..... *D. parumapertus* (See figure 28)

Known from lowlands of southern Idaho, southeastern Oregon, east of the Sierra Nevada mountains in California, all of the lowlands of Nevada, Utah, western Colorado, Arizona, New Mexico, western Texas, western Oklahoma, and northern Mexico. The larval stage is found on practically all the smaller vertebrates distributed in the areas above. The adults are almost invariably found on the Black-tailed jack rabbit, *Lepus californicus*, but at certain seasons adults, nymphs, and larvae may be taken from this host. This is without doubt the most abundant *Dermacentor* tick distributed in the lowland regions of the Great Basin states.



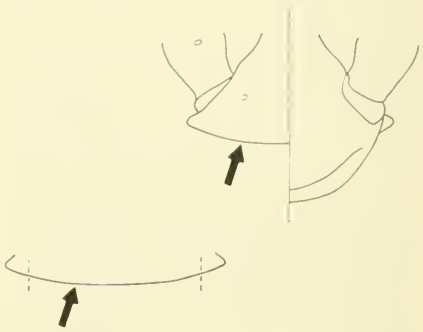
Spur on coxa I moderately tapered 4

4. Posterior margin of basis capituli straight to slightly concave. Sensilla porosa present. Sides of cervical grooves not parallel ..... *D. occidentalis* (See figure 24)



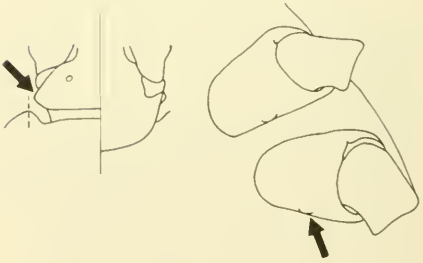
Distribution limited more or less to plains region of northern California and southwestern Oregon. Knowledge of host-parasite association for immature ticks of this species shows a wide variety of smaller vertebrates.

Posterior margin of basis capituli weakly curved. Best observed on unmounted specimens ..... *D. andersoni* (See figure 12)



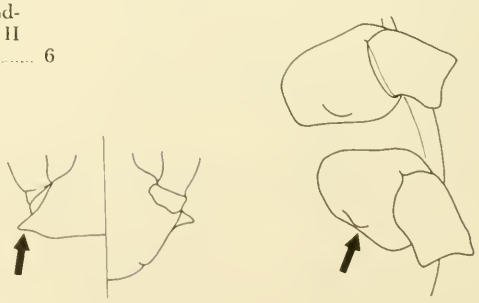
Known from mountainous areas in northern Utah, Nevada, and eastern slopes of the coastal range in northern California. Mountain areas are generally interpreted as above 5,000-foot elevations above sea level. Ticks are also in both mountain and lowland areas of eastern Oregon, eastern Washington, most of Idaho, Wyoming, Montana, and western Canada. Hosts for the larvae constitute a great number of species of smaller mammalian vertebrates distinctive for the geographic area where the tick species is distributed.

5. Basis capituli with lateral points much reduced, not extending beyond the scapulae. Spurs on coxae II and III very indistinct ..... *D. albipictus* (See figure 8)



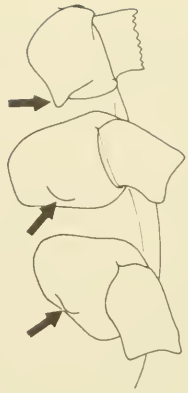
Single host tick. If immature ticks are collected during winter months from large vertebrate hosts, they most likely will be this species.

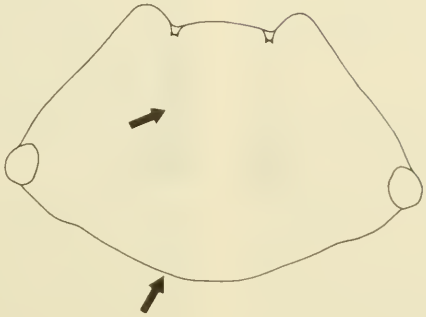
Basis capituli with lateral points extending beyond scapulae. Spurs on coxae II and III distinct 6



6. Spur on coxa I acute. Spurs on coxae II and III not extending beyond posterior margin of plate. Margins of cervical grooves parallel. Best observed on unmounted specimens. Posterior margin of scutum prominently curved .... *D. variabilis* (See figure 32)

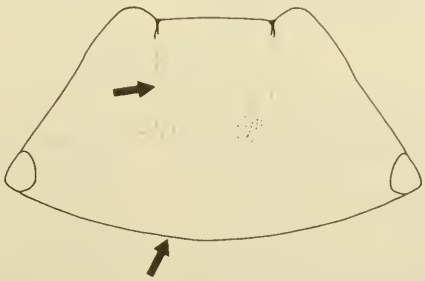
Very little known about the host-parasite relationships in the larval stage for this species in the western United States.





Spur on coxal plate I sub-acute. Spurs on coxae II and III postmarginal. Margins of cervical grooves divergent. Best observed on unmounted specimens. Posterior margin of scutum slightly curved ..... *D. hunteri* (See figure 20)

Little known about the host-parasite relationships in the larval stage for this species of tick.



CONCLUSIONS

Several thousand specimens of larval, nymphal and adult ticks of the genus *Dermacentor* distributed in the western United States have been examined. The main emphasis was centered on selected anatomical and morphological features. Nevertheless such factors as geographic distribution, host parasite relationships and altitudinal distribution have been considered. This has all been done in order to contribute to information which will facilitate specific identification of *Dermacentor* ticks in their various developmental stages of growth. More obvious conclusions which may be drawn from this study are as follows:

1. Those features used by previous workers for specific separation of adults and nymphs are for the most part reliable. There is still enough variation within species and between some species to create problems. Therefore, it will still be necessary to adjust identification descriptions by the inclusion of localized features to fit the needs when a specific identification is made. For example, the degree of coxal spur divergence is somewhat variable. Yet this feature plus altitudinal distribution and host parasite relationship for a given locality will provide a more accurate identification.
2. For specific identification of nymphs such features as the shape of the anterolateral margin of the basis capituli and the position and form of the lateral points, length and width of palpi, shape of the spiracular plate, size of goblet cells, size, shape and position of internal and external spurs on coxa I, size and form of the cervical groove are reliable characteristics which may be used.
3. For the specific identification of larvae the following may be reliably used, accompanied by other characteristics: Dermal sensilla, shape, position and size of lateral points, form of the basis capituli, general morphology of the cervical grooves, shape of the posterior scutal margin, and the size, form and position of the coxal spurs.
4. Reliance on geographic distribution and host parasite relationships is still needed in making specific identification of all stages. This requires concentrated life history studies of all of the known species examined on a basis of ecologically similar geographic regions. This is true with some of our better-known species such as *D. andersoni*, *D. parumapertus* and *D. occidentalis*. For such species as *D. halli* and *D. hunteri* little is known about their life cycles under natural conditions.
5. The illustrated keys and descriptions in this study should help provide a better understanding of the species of *Dermacentor* ticks in the western U.S. It is our plan for subsequent studies to examine each species in each developmental stage in our collections, using the present study as the principal vehicle of analysis. Each species will be studied separately, and the information will be published as individual separate papers, including all data we have accumulated plus that made available to us, as well as from the literature. It is hoped that other workers may find the present paper useful for purposes of identification of *Dermacentor* ticks in the western U.S. In due process of time certainly the combined efforts of several workers will materially unravel and reveal a more accurate understanding of the biology of the stages of development for ticks in the western U.S., not only for *Dermacentor*, but for all species of ticks as well.

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